

# Heterogeneous climatic controls on tropical-forest biomass

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Tropical-forest aboveground biomass (AGB) is a major component of the global carbon cycle and understanding its response to climate change is crucial for predicting future climate–carbon feedbacks. Yet debate continues as to whether differences between studies in observed associations with climate reflect true regional variation or methodological differences<sup>1–5</sup>. Here we analyse around 16 million spaceborne-LiDAR-derived estimates of AGB for the year 2020 across intact lowland forests in the Amazon, the Congo Basin and Southeast Asia to investigate how climatic variables differentially relate to AGB on pantropical scales. We show that climatic associations with AGB are heterogeneous and depend on environmental context. Temperature dominates in drier forests, with AGB in the Congo Basin the most sensitive to warming, whereas Southeast Asian forests have the strongest declines in AGB under increasing water limitation. Across regions, the effects of temperature and drought anomalies intensify with aridity and are further modified by soils and topography. In the tallest (above 70 m), carbon-dense forests<sup>6,7</sup>, storms (lightning and windthrow) emerge as a strong negative driver. These results reconcile previously conflicting findings and show that predicting tropical-forest carbon storage requires accounting for interactions among climate, disturbance, soil and topography in a variety of biogeographical contexts.

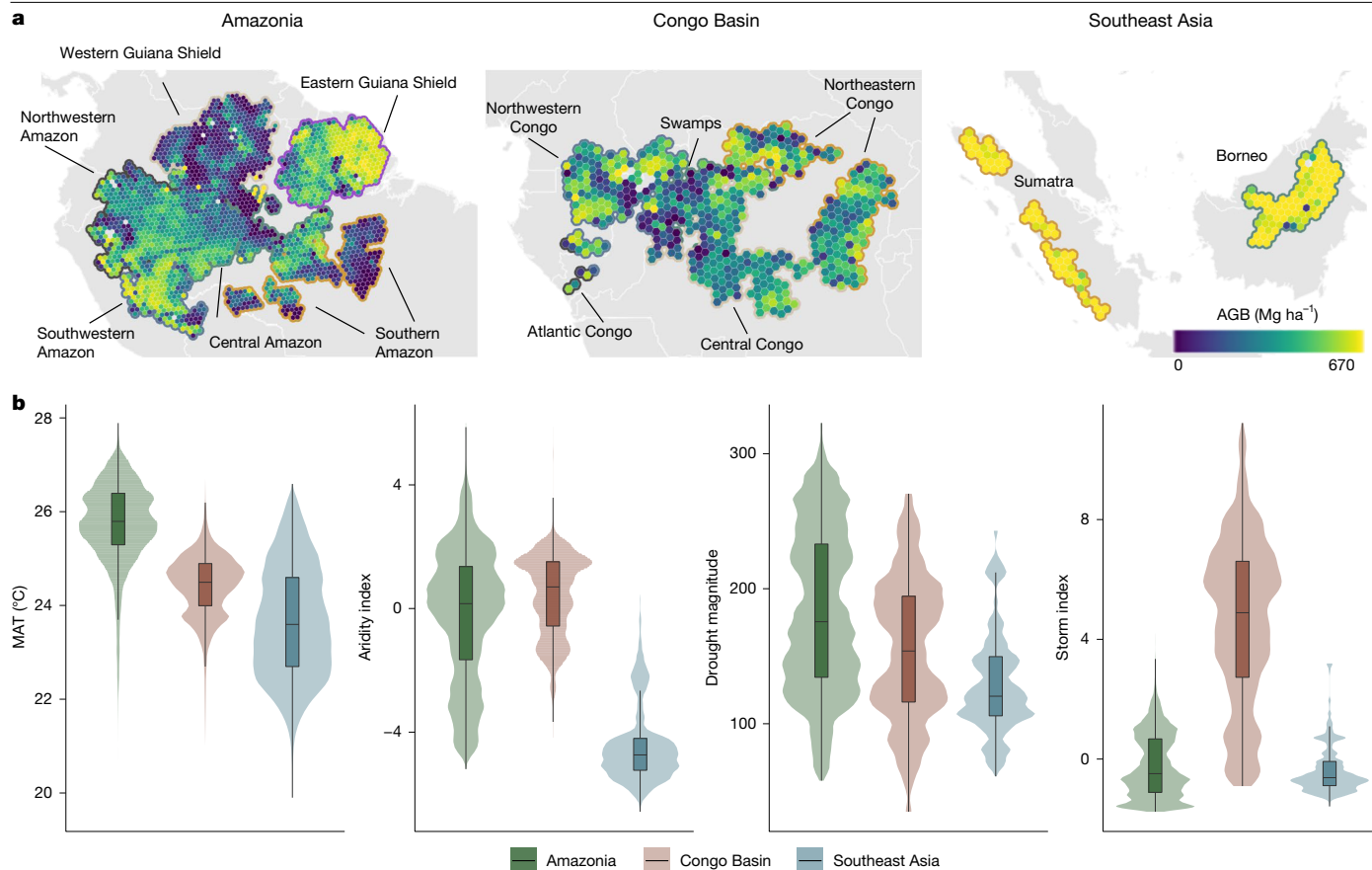
The aboveground biomass (AGB) of tropical forests is a major component of the global carbon cycle<sup>8</sup>. It reflects the net balance of forest productivity with tree mortality and branchfall, each shaped by floristic composition, environmental variation and global change<sup>9</sup>. There is wide variation in carbon stocks across intact lowland tropical forests, both within and between continents<sup>10</sup>. Although much progress has been made in understanding the influences of the environment on AGB variation at local scales<sup>5</sup>, ground plots sample only a tiny proportion (less than 0.001%) of tropical-forest area and constitute a highly uneven sample, with major geographical gaps<sup>11</sup>. Therefore, we might have a skewed understanding of how much carbon tropical forests can store, because ground-based plots oversample relatively accessible sites, which are also characterized by distinct environmental conditions, land-use legacies and disproportionately large amounts of archaeological evidence of past human activities<sup>12,13</sup>.

The effects of environmental variables on AGB can shift in magnitude and direction at local and regional scales<sup>14</sup>, and thus a complete understanding of environmental influences requires relatively dense and spatially distributed observations. Plot-based studies have provided valuable insights into the effects of temperature<sup>3,4</sup> and water availability<sup>1,2</sup>, and some have also investigated storm-related drivers and their interactions with other environmental factors<sup>15</sup>. However, differences in plot locations, spatial coverage and sampling intensity can make it challenging for field studies to capture the full range of environmental variability and the interactions among environmental

drivers across tropical forests. A more complete understanding of environmental influences on AGB is crucial for assessing the carbon benefits of protecting tropical forests and Earth system vulnerability to global change.

Most Earth system models assume that environmental effects on tropical-forest AGB are consistent everywhere<sup>9,16</sup>, but climate, geology, topography, evolutionary history and biogeography jointly lead to complex variation in AGB<sup>17,18</sup>. Resource availability (for example, soil nutrients, water availability and solar radiation) and disturbance regimes (for example, prolonged droughts and lightning) interactively influence demographic processes that control AGB. Water availability is key for supporting the growth and maintenance of tall trees, which are particularly vulnerable to cavitation during periods of prolonged droughts<sup>19</sup>. However, high rainfall is generally associated with frequent cloud cover, which limits photosynthesis, and the development of deep convective clouds, which is linked to lightning and high-velocity downdrafts (downbursts) that increase the probability of windthrows and tree damage<sup>20–23</sup>. Similarly, solar radiation is a fundamental resource, but high solar radiation is associated with high temperatures and increased evaporative demand, which can reduce water availability and growth and increase tree mortality<sup>4,24</sup>. Soils and topography influence plant growth and defence strategies and further modulate climate effects, in part owing to associated variation in functional composition<sup>25</sup>. However, it remains unclear which combinations of climatic factors most strongly limit the AGB of anthropogenically

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**Fig. 1 | Pantropical variation in AGB and climate variables in intact lowland tropical forests in three biogeographical regions.** **a**, Spatial variation in mean AGB in lowland intact forests estimated from GEDI spaceborne LiDAR in 2020 across 13 ecoregions. Each hexagonal point corresponds to a grid cell of around  $1,770 \text{ km}^2$  (approximately  $50 \times 50 \text{ km}$ ). The number of footprints across intact lowland tropical forests varies among grid cells, reflecting land use and availability of GEDI data (Extended Data Fig. 10). **b**, Variation within each biogeographical region in four climatic drivers: MAT, an aridity index, drought magnitude and a storm index. The aridity and storm indices represent dimensions of variation derived from separate PCAs, with aridity capturing

precipitation seasonality, temperature seasonality, water deficit throughout the year and solar radiation, and storms capturing lightning frequency and CAPE (associated with windthrow probability). Drought magnitude is calculated as the absolute value of the cumulative sum of SPEI values below  $-1$  on a 180-day timescale for the years 1980–2019, thereby integrating both the duration and the intensity of drought events in the previous 40 years. Sample sizes: Amazon  $n = 216,667$ ; Congo Basin  $n = 40,306$ ; Southeast Asia  $n = 29,436$ . In box plots, the centre line indicates the median, the box bounds are the 25th and 75th percentiles (interquartile range; IQR) and the whiskers extend to the most extreme values within  $1.5 \times \text{IQR}$  of the box bounds.

undisturbed forests within and between biogeographical regions. The relative importance of climatic drivers might shift under different environmental conditions, but how these shifts manifest spatially is poorly understood. More information about the underlying processes that drive biomass variation is necessary to improve Earth system model predictions of current spatial variation and our comprehension of forest responses to environmental changes<sup>16</sup>.

### AGB variation in intact tropical forests

We used 16 million remotely sensed AGB estimates across intact tropical forests from the Global Ecosystem Dynamics Investigation (GEDI) spaceborne light detection and ranging (LiDAR) mission<sup>26</sup> for the year 2020 to elucidate the interacting influences of mean annual temperature (MAT), aridity, drought magnitude and storms, and how their relationships with AGB vary with topography and soil at landscape scales. An intact forest landscape is defined as a continuous mosaic of forest ecosystems with no remotely detected signs of human activity that occupies a minimum area of  $500 \text{ km}^2$  and is at least  $10 \text{ km}$  wide at the broadest place<sup>27</sup>. GEDI AGB estimates are derived from LiDAR-based relative canopy heights, which are excellent predictors of spatial variation in AGB in tropical forests<sup>28</sup>. However, they are not perfect, because forests with the same canopy

height can differ in biomass owing to variation in trunk diameters and wood densities<sup>29</sup>.

AGB in intact lowland tropical forests is highly variable and strongly spatially structured within and across regions (Fig. 1a). Our sampling spans the entire range in AGB across intact lowland forests in Amazonia, the Congo Basin and Southeast Asia (Fig. 1a). Mean AGB estimates ( $\pm \text{s.d.}$ ) in intact lowland forests were  $222 \pm 75 \text{ Mg ha}^{-1}$  in the Amazon,  $226 \pm 63 \text{ Mg ha}^{-1}$  in the Congo Basin and  $370 \pm 107 \text{ Mg ha}^{-1}$  in Southeast Asia. We aggregated GEDI footprint-level AGB estimates to average values for  $2.5 \times 2.5\text{-km}$  grid cells for analyses of the relationship of AGB with climate, topography and soils. This reduced the measurement noise and sampling uncertainty that are inherent in individual footprints<sup>30</sup>, and improved alignment between biomass estimates and the coarse spatial scale of climatic driver data. Subsequent landscape-scale analyses were done using around 285,000 values for  $2.5 \times 2.5\text{-km}$  grid cells (around 215,000 for the Amazon, 40,000 for the Congo Basin and 30,000 for Southeast Asia). We also present footprint-level analyses for each ecoregion in Extended Data Fig. 1 to show relationships between the environment and AGB at finer spatial scales.

We first performed two principal component analyses (PCAs) to define axes representing aridity and storms (Extended Data Fig. 2a,b). Higher values on the aridity axis indicate more seasonal and arid

conditions, marked by a more negative (lower) maximum climatological water deficit (MCWD); higher intra-annual variability in precipitation and temperature, marked by longer dry periods (more months with precipitation lower than 100 mm); and higher numbers of clear-sky days (a proxy for direct solar radiation). By contrast, lower values on this axis indicate aseasonal climates with higher mean annual precipitation (MAP), heavy rains with at least 20 mm of precipitation daily and a minimal water deficit throughout the year. Aridity thus captures typical seasonal water deficits (Extended Data Fig. 2a). Our storm index is based on co-varying lightning frequency and convective available potential energy (CAPE). Because CAPE values higher than  $1,023 \text{ J kg}^{-1}$  are associated with an eightfold higher probability of windthrow, compared with lower values<sup>23</sup>, we emphasized extreme convective conditions by including first- and second-order terms of excess CAPE (defined as CAPE values higher than  $1,023 \text{ J kg}^{-1}$ ) (Extended Data Fig. 2b). Higher values of the storm index indicate regions with higher frequencies of lightning and windthrows<sup>21,31,32</sup>. Note that this storm index does not include tropical cyclones, which are exceedingly rare in lowland tropical forests and essentially absent in our study areas.

We then fitted linear mixed-effects (LME) models for tropical-forest AGB using a combination of backward selection and the least absolute shrinkage and selection operator (LASSO) method, which fits a regression model while preventing overfitting by penalizing coefficient size, keeping only the most informative predictors. We tested direct effects and interactions of climatic, edaphic and topographical predictors, with separate models fitted in each biogeographical region (the Amazon, the Congo Basin and Southeast Asia). We included MAT, aridity, drought magnitude, storms, clay content, cation exchange capacity (CEC), topographical position index (TPI; at 150 m and 1,000 m scales, indicating topographical position from ridges and interfluvies to valleys) and slope. Here, drought magnitude is defined as the absolute value of the sum of standardized precipitation–evapotranspiration index (SPEI) values below  $-1$  on a 180-day timescale, integrating the duration and intensity of drought events between 1980 and 2019. It therefore characterizes long-term exposure to drought rather than any single event; it is strongly related to the intensity of El Niño events<sup>33</sup>.

These environmental variables were mostly uncorrelated (Extended Data Figs. 3–5). Log-transformed and quadratic terms included in the LME model captured non-linear relationships between AGB and environmental variables (Supplementary Figs. 4–6), and we also tested first-order interactions. Each LME model included random effects for ecoregions (six ecoregions in the Amazon, five ecoregions in the Congo Basin and two ecoregions in Southeast Asia; Fig. 1a) and for  $50 \times 50$ -km grid cells nested within ecoregions, to account for spatially autocorrelated biogeographical differences including those due to species and functional composition<sup>34</sup>.

## Climatic relationships with AGB

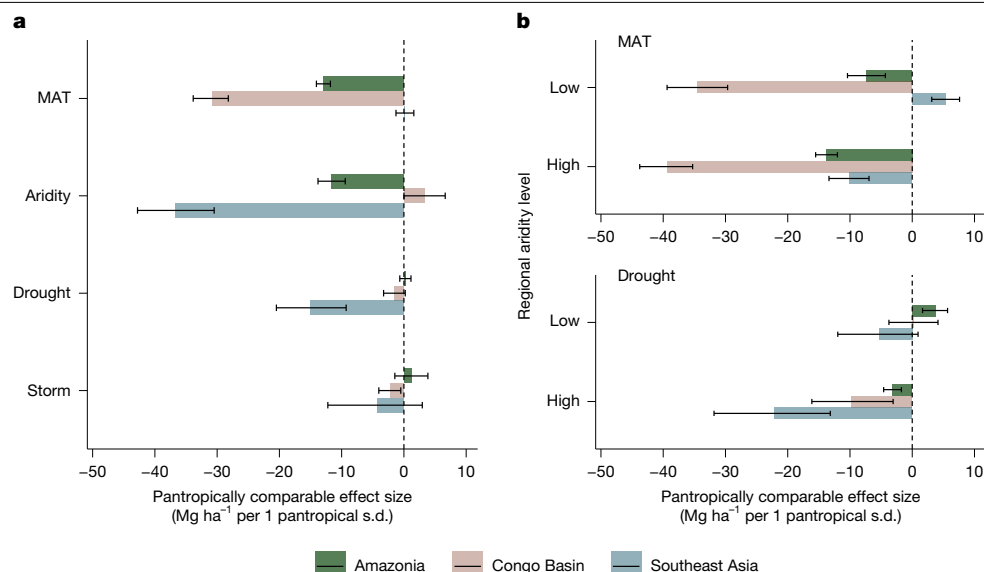
Climatic variables were associated with variation in tropical-forest AGB across all regions, with landscape-scale patterns mainly consistent with mechanisms proposed in previous studies (Table 1), but the magnitude and direction of these associations varied. In the Amazon and the Congo Basin, temperature had the strongest negative effect, whereas in Southeast Asia, aridity (typical seasonal water limitation), drought magnitude and storms had the strongest negative effects (Fig. 2). The lower vulnerability of Amazonian and Congo Basin forests to water limitation, relative to Southeast Asian forests, is likely to reflect long-term climatic legacies, because past environmental conditions favoured the persistence of more drought-tolerant species<sup>17,35</sup>. Stand-level analysis for each ecoregion reveals the major effects of storms on AGB in Southeast Asia and the eastern Guiana Shield, which highlights the importance of disturbances from lightning and convective winds in shaping the AGB of tall forests dominated by trees

**Table 1 | Predicted relationships, hypothesized ecological and physiological mechanisms and results from this study on the effects of temperature, aridity, drought magnitude and storms on AGB in intact lowland tropical forests**

|                                                                               |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
|-------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>Temperature (MAT)</b>                                                      |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| <b>Prediction:</b>                                                            | negative effect on AGB and a strong negative interaction with aridity                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| <b>Mechanism:</b>                                                             | higher temperatures increase vapour pressure deficit (VPD), leading to stomatal closure, reduced photosynthesis, hydraulic stress and higher tree mortality, especially where water availability is lower <sup>33,62,63</sup>                                                                                                                                                                                                                                                                                                                                                                                       |
| <b>Results:</b>                                                               | Amazon: strong negative effect<br>Congo Basin: very strong negative effect and strong negative interaction with aridity<br>Southeast Asia: no significant direct effect, but strong negative interaction with aridity<br>Overall, significant interaction effects of temperature with aridity, soil and topography across all regions                                                                                                                                                                                                                                                                               |
| <b>Aridity (precipitation seasonality, water deficit and solar radiation)</b> |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| <b>Prediction:</b>                                                            | mostly negative effect on AGB; effects might be non-linear                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| <b>Mechanism:</b>                                                             | high aridity (long dry seasons) directly decreases productivity because lack of water causes many plant species to become deciduous or to shut down leaves (close stomata), and can increase tree mortality <sup>41</sup> . At the opposite extreme, very low aridity (everwet) is associated with high cloud cover and reduced solar radiation, reducing productivity <sup>24,45</sup> . Under intermediate aridity (short dry seasons), many plants and species can maintain access to water and benefit from increased solar radiation, maximizing productivity                                                  |
| <b>Results:</b>                                                               | Amazon: non-linear relationship; AGB peaks at intermediate aridity (negative effects of aridity <sup>2</sup> )<br>Congo Basin: positive direct effect with negative effects at higher temperature (strong negative interaction effect with temperature)<br>Southeast Asia: very strong negative effect, despite the lower aridity relative to other tropical regions                                                                                                                                                                                                                                                |
| <b>Drought magnitude (SPEI anomalies)</b>                                     |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| <b>Prediction:</b>                                                            | negative effect on AGB                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| <b>Mechanism:</b>                                                             | severe droughts (much drier than normal for a site) can cause hydraulic failure and carbon starvation, reducing productivity and increasing mortality, and thus reducing AGB <sup>33</sup>                                                                                                                                                                                                                                                                                                                                                                                                                          |
| <b>Results:</b>                                                               | Amazon: drought interacts strongly with aridity, reducing AGB in more arid forests but increasing it in everwet (radiation-limited) forests<br>Congo Basin: no significant effect or interaction with aridity<br>Southeast Asia: very strong negative effect, and a strong negative interaction with aridity, meaning that drought effects are exacerbated in arid forests                                                                                                                                                                                                                                          |
| <b>Convective storms (lightning+CAPE)</b>                                     |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| <b>Prediction:</b>                                                            | negative effect on AGB                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| <b>Mechanism:</b>                                                             | lightning strikes and convective winds cause tree mortality through snapping, uprooting and crown damage, reducing woody residence time and thus AGB <sup>21,31,32</sup>                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| <b>Results:</b>                                                               | Amazon: no direct effects, but strong negative interaction with temperature, meaning that storm effects are more negative in warmer forests<br>Congo Basin (most intense storms): weak negative effect<br>Southeast Asia: no direct effects, but very strong negative storm effects in arid forests<br>Overall, significant interaction effects of storms with aridity or temperature across all regions. Footprint-based analyses for each ecoregion reveal very strong negative storm effects in some very tall forests (exceeding a height of 70 m; including eastern Guiana Shield and Sumatra, but not Borneo) |

exceeding a height of 70 m (Extended Data Fig. 12, based on footprint-level analysis).

The climatic impacts were strongly dependent on environmental context. Declines in biomass with temperature and drought were stronger in more arid areas (Fig. 2), and topography and soil properties further mediated climatic effects across tropical forests (Extended Data Figs. 6–8). These results show that no single factor explains the spatial variation in AGB; instead, it reflects the combined influences of



**Fig. 2 | Normalized climatic effects on tropical-forest AGB across biogeographical regions. a**, Climatic effect of MAT, aridity (seasonal water stress), drought and storms on AGB, normalized per one pantropical standard deviation (s.d.) of each variable, by biogeographical region. Effects were calculated as the difference in predicted AGB between the 90th and 10th percentiles of each climatic predictor, rescaled to the pantropical s.d. All error bars correspond to mean  $\pm$  95% confidence intervals. Note that AGB peaks at intermediate aridity (around the 30th percentile) in the Amazon (quadratic effect); therefore, we contrast the 90th with the 30th percentile to capture the declining effect. **b**, Variation in the effects of MAT and drought with regional

aridity. Low and high aridity represent forests at the 10th and 90th percentiles of regional aridity (aridity corresponds to a dimension obtained by PCA:  $-3.4$  to  $2.2$  in the Amazon,  $-1.4$  to  $1.9$  in the Congo Basin and  $-5.6$  to  $-2.3$  in Southeast Asia). Sample sizes: Amazon  $n = 216,667$ ; Congo Basin  $n = 40,306$ ; Southeast Asia  $n = 29,436$ . LME models incorporated first- and second-order (squared-term) effects of these climatic variables, together with soil variables (clay content and CEC) and topographical variables (TPI at 150 m and 1,000 m, and slope), as predictors, along with their two-way interactions, as well as random effects for  $50 \times 50$ -km grid cells nested within ecoregions.

several environmental variables. We provide standardized regression coefficients and full model summaries for the landscape-scale analyses in Supplementary Tables 1–3.

Our models explained 53–72% of the variation in AGB at the landscape scale. At the footprint level, uncertainties were much higher, with an  $R^2$  value of 25% for all three biogeographical regions, indicating the scale dependence of relationships between biomass and climatic variables. The fixed environmental effects (climate, soils and topography) explained 14–20% of AGB variation within each biogeographical region, whereas the spatial random effects for ecoregions and  $50 \times 50$ -km grid cells together explained 33–57% of variation (fixed, ecoregion and grid-cell effects: 14%, 22% and 35% in the Amazon; 20%, 1% and 40% in the Congo Basin; and 20%, 10% and 23% in Southeast Asia). Therefore, much of the spatial variation in the AGB of intact forests reflects biogeographical and landscape-scale differences that the included climate, soil and topography variables alone do not capture.

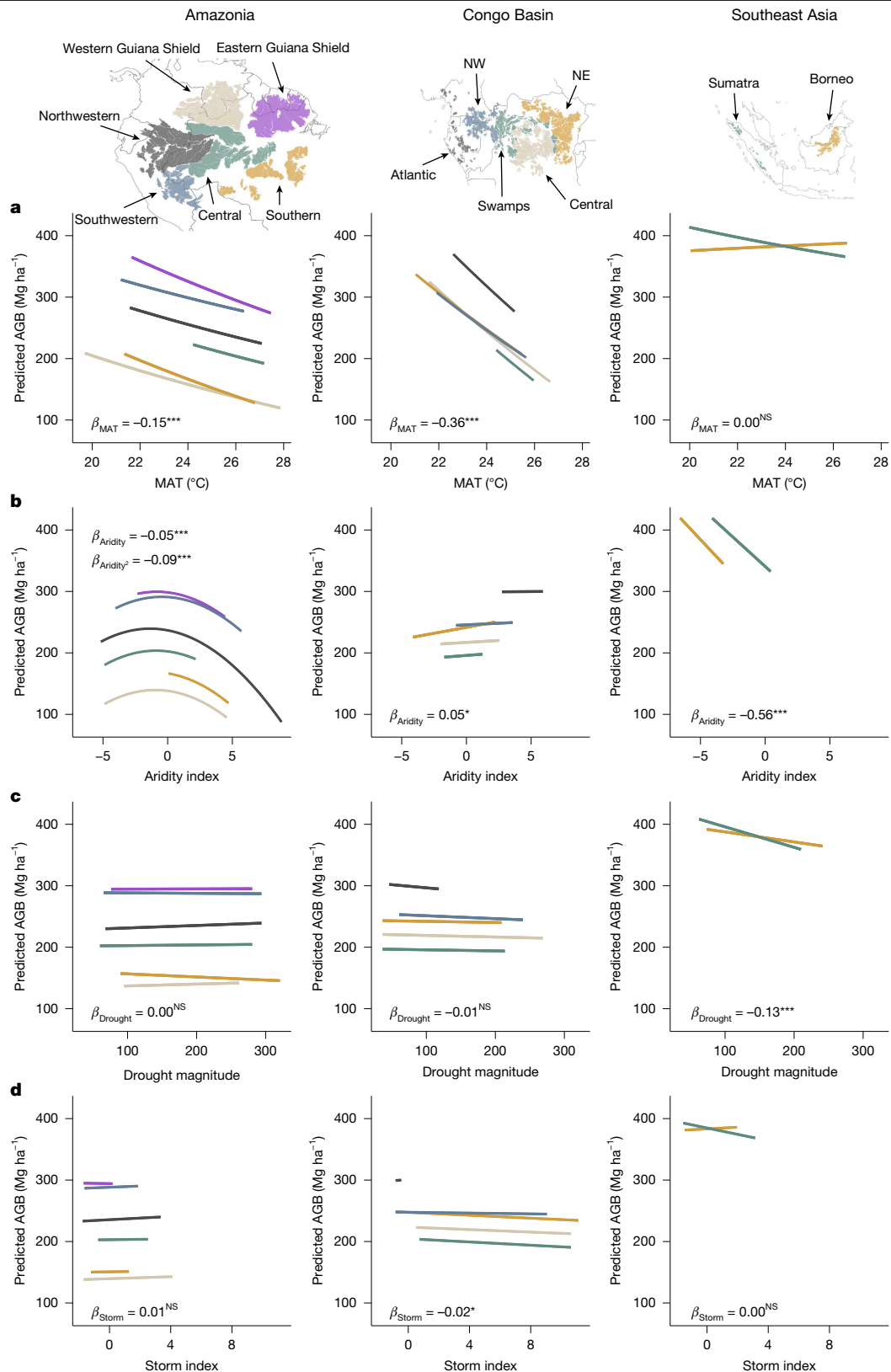
In addition, large unexplained variance remains. The cross-validated  $R^2$  of our models computed on held-out data was 45%, 32% and 28% for the Amazon, the Congo Basin and Southeast Asia, respectively. Random forest models using the same environmental predictors alongside latitude and longitude resulted in comparable cross-validated  $R^2$  values (48%, 35% and 31%) (Supplementary Methods 5), suggesting that nonlinearities or interactions contribute little to residual variance. Residual variance could therefore be a result of (i) AGB being a snapshot of ongoing forest dynamics, with trees dying, growing and recruiting through partly stochastic processes after natural disturbances<sup>36</sup>; (ii) high spatial heterogeneity in tropical-forest structure within the 2.5-km grid cells, which is caused by local variation in topography, soils and microclimate and which coarse-resolution predictors do not resolve<sup>37</sup>; and (iii) our explanatory variables being themselves imperfect; better climate and soil metrics might explain a larger proportion of the variation.

Temperature was the single most important climate variable in Amazonia and the Congo Basin, with substantial negative standardized

coefficients for log-transformed MAT (Fig. 3a;  $\beta_{\text{Amazonia}} = -0.15$ ,  $\beta_{\text{Congo}} = -0.36$ , with all  $P$  values  $< 0.0001$ ), whereas Southeast Asian forests had no significant direct effects ( $\beta_{\text{SE Asia}} = 0.00$ ,  $P = 0.9$ ). Temperature also had strong negative interactions with aridity (aridity  $\times$   $\ln(\text{MAT})$ ):  $\beta_{\text{Amazonia}} = -0.02$ ,  $P = 0.0082$ ;  $\beta_{\text{Congo}} = -0.11$ ,  $P < 0.0001$ ;  $\beta_{\text{SE Asia}} = -0.10$ ,  $P < 0.0001$ ). Thus, under high aridity, higher temperatures were associated with lower biomass across all biogeographical regions (Fig. 4a–c). Negative effects of temperature and negative interactions with aridity are consistent with hypothesized mechanisms involving decreased productivity and increased tree mortality, owing mainly to the associated increase in vapour pressure deficit (VPD) or atmospheric dryness (Table 1). Previous analyses of tree census data for 590 tropical-forest plots<sup>4</sup> found that sites with a higher maximum temperature had substantially lower AGB and woody productivity, and that the combination of higher temperature and higher aridity led to lower biomass residence. Our analyses of a much larger dataset also found consistently negative effects of temperature, and revealed strong regional variation in this thermal sensitivity.

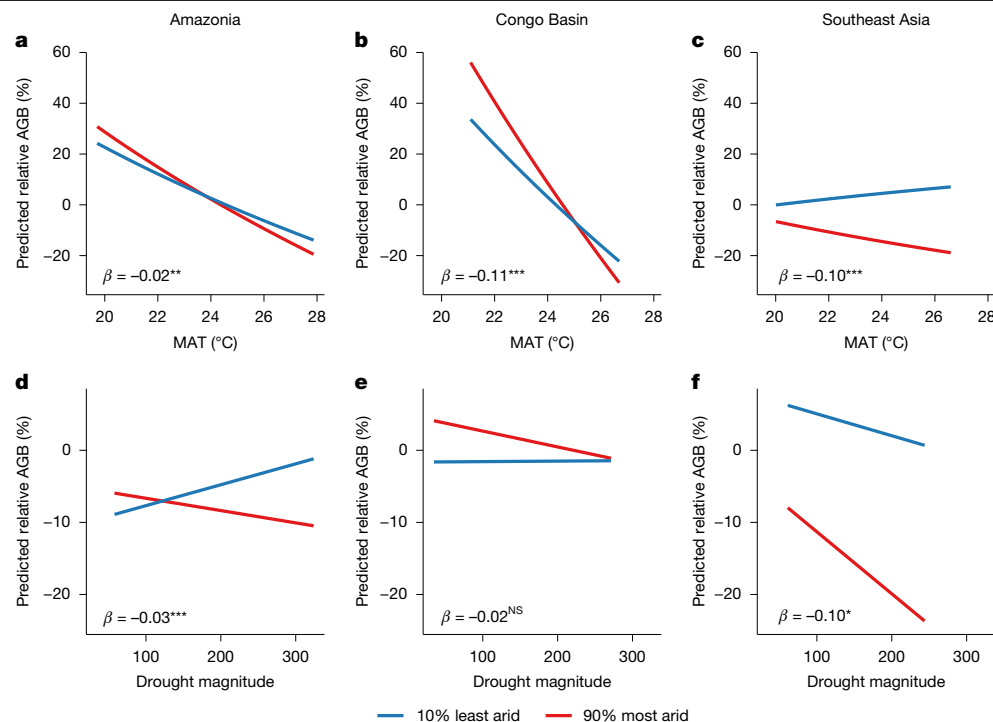
The thermal sensitivity of AGB is 2.5 times higher in the Congo Basin than it is in the Amazon, whereas there is no evidence for thermal sensitivity in cooler Southeast Asia (regional mean temperatures are  $25.7^\circ\text{C}$  in the Amazon,  $24.4^\circ\text{C}$  in the Congo Basin and  $23.6^\circ\text{C}$  in Southeast Asia). Among forests in each region, a  $1^\circ\text{C}$  higher MAT is associated with  $27.6 \text{ Mg ha}^{-1}$  lower AGB in the Congo Basin,  $11.0 \text{ Mg ha}^{-1}$  lower AGB in the Amazon and  $0.1 \text{ Mg ha}^{-1}$  lower AGB in Southeast Asia (if all other variables are held at their regional means). The larger thermal sensitivity of the Congo Basin forests might in part reflect regional differences in current temperatures and aridity, as well as different evolutionary and biogeographical histories that shape species composition and functional traits<sup>38</sup>. Soil properties and topography also had a key role in modulating the effects of temperature in both the Amazon and the Congo Basin, resulting in locally heterogeneous buffering or amplification of temperature influences (Extended Data Figs. 6–8).





**Fig. 3 | Partial climatic effects on AGB among ecoregions in the Amazon, the Congo Basin and Southeast Asia.** We show how predicted AGB varies (while holding all covariates constant at their mean value within each ecoregion) with MAT (a), the aridity index that is related to seasonality in precipitation and temperature, maximum water deficit within a year and clear-sky days (b), drought magnitude derived from the SPEI (c) and the storm index (d).  $\beta$  is the standardized regression coefficient for the respective climatic variables

obtained from LME models, and asterisks indicate two-sided significance:  $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ , NS, not significant. Exact  $P$  values obtained from two-sided tests of fixed effects in the LME models are provided in Supplementary Tables 1–3; no adjustment was made for multiple comparisons. Line colours correspond to ecoregions. Sample sizes: Amazon  $n = 216,667$ ; Congo Basin  $n = 40,306$ ; Southeast Asia  $n = 29,436$ . The partial effects of soil and topographical variables on AGB are also presented in Extended Data Fig. 11.



**Fig. 4 | Temperature and drought effects depend on aridity across all biogeographical regions.** Here we show predicted AGB from LME models, relative to the regional mean AGB, as a function of MAT (a–c) and drought (d–f), and how these relationships shift across aridity levels (colours) and differ among regions (columns: Amazonia (a,d), Congo Basin (b,e) and Southeast Asia (c,f)). Blue and red lines represent forests in the 10th and 90th percentile of regional aridity, respectively (aridity axis based on a PCA varied between  $-3.4$  and  $2.2$  for the Amazon,  $-1.4$  and  $1.9$  for the Congo Basin, and  $-5.6$  and  $-2.3$  for Southeast Asia). Predicted relative AGB varied significantly with the interactions between log-transformed MAT and aridity (a–c), and drought

magnitude and aridity (d–f), indicating that each main effect was modified by aridity.  $\beta$  is the standardized regression coefficient for the environmental variable shown on the x axis. Exact  $P$  values obtained from two-sided tests of fixed effects in the LME models:  $P = 0.0082$  (Amazon),  $P < 0.0001$  (Congo Basin) and  $P < 0.0001$  (Southeast Asia) for the  $\ln(\text{MAT}) \times \text{aridity}$  interaction, and  $P < 0.0001$  (Amazon),  $P = 0.2341$  (Congo Basin) and  $P = 0.0130$  (Southeast Asia) for the drought  $\times$  aridity interaction. No adjustment was made for multiple comparisons. Sample sizes: Amazon  $n = 216,667$ ; Congo Basin  $n = 40,306$ ; Southeast Asia  $n = 29,436$ . Interactions among all environmental variables are shown in Extended Data Figs. 6–8.

Water deficits related to aridity and drought magnitude also exert widespread influences on AGB (Fig. 3b,c), with variable effects across the tropics. Southeast Asian forests exhibited the strongest linear declines in AGB with increasing aridity ( $\beta = -0.56$ ,  $P < 0.0001$ ) and more intense droughts ( $\beta = -0.13$ ,  $P < 0.0001$ ), despite having the mildest aridity and drought anomalies of the three biogeographical regions. On average, these forests experience only  $0.4 \pm 0.6$  months per year in which precipitation is less than 100 mm, and they have a lower drought magnitude ( $129 \pm 37$ ) than do forests in the Amazon ( $183 \pm 60$ ) and the Congo Basin ( $155 \pm 52$ ). These results indicate that Southeast Asian forests have a low tolerance of moisture limitation, even under short intra-annual dry seasons. In many parts of Southeast Asia, dry periods are associated with occasional strong El Niño events and are relatively unpredictable, occurring in some years and not others, with variable seasonal timing. This climatic unpredictability, combined with a relative dearth of traits that convey tolerance to seasonal droughts and a high endemism of tall dipterocarps adapted to high water availability, make Southeast Asian forests particularly vulnerable to higher water limitation, in comparison with Amazonian and Congolian forests<sup>39,40</sup> (Fig. 4f).

In Amazonia, where the greatest range of aridity levels was observed, we found a significant quadratic effect of aridity (aridity:  $\beta = -0.05$ ; aridity<sup>2</sup>:  $\beta = -0.09$ ; all  $P$  values  $< 0.0001$ ), with AGB peaking at moderate values (when the aridity axis is  $-0.8$ , which corresponds to an average of  $2.5 \pm 0.5$  months per year with less than 100 mm of precipitation). Moderate aridity is likely to relieve light limitation owing to increased solar radiation (decreased cloudiness), while inducing little water limitation in this region because of the combination of shorter dry seasons and a flora that has been selected to withstand such conditions by historical

exposure to seasonal droughts<sup>41</sup>. More intense aridity caused by longer dry seasons leads to substantial declines in AGB, because prolonged dry seasons can increase tree mortality and reduce growth in the Amazon<sup>42</sup>. The wettest areas of the Amazon also have lower AGB, which could reflect a combination of light limitation (low solar radiation), more-frequent extreme rainfall events (increasing tree mortality) and an increased predominance of species with low investments in hydraulic safety and high woody biomass turnover rates<sup>17,43,44</sup>.

The effects of more drought varied with aridity across the Amazon, with arid forests showing strong negative effects and everwet forests showing positive effects (Fig. 4d; drought:  $\beta = 0.01$ ,  $P = 0.01$ ; drought  $\times$  aridity:  $\beta = -0.03$ ,  $P < 0.0001$ ). An increase in AGB with drought was observed in aseasonal, everwet conditions in parts of northwestern Amazonia and the western Guiana Shield with annual precipitation levels higher than 3,200 mm. Although tree species in the everwet forests might be more vulnerable to drought owing to lower wood density and less embolism-resistant xylem<sup>17</sup>, moderate drying reduces cloud cover and increases incoming solar radiation, which could increase carbon gain provided that trees maintain hydraulic function, tissue maintenance and defence<sup>45,46</sup>. Indeed, tropical forests receiving more than around 2,000 mm of rainfall per year with deep rooting systems can sustain evergreen canopies during more prolonged droughts<sup>18,24,41,45</sup>, suggesting that light rather than water constrains productivity in these everwet regions of the Amazon. Together, these results suggest a conditional resilience to drought anomalies in the Amazon. Nevertheless, continued longer dry seasons could shift this balance, reducing drought-induced productivity gains and increasing vulnerability across the Amazon<sup>33</sup>.

In the Congo Basin, forest biomass increased with aridity ( $\beta = 0.05$ ,  $P = 0.05$ ), despite some ecoregions experiencing more than 4 dry months per year with less than 100 mm of rainfall (Extended Data Fig. 9). However, the interaction between aridity and temperature was strongly negative (aridity  $\times$   $\ln(\text{MAT})$ :  $\beta = -0.11$ ,  $P < 0.001$ ), such that biomass declined with aridity in higher temperatures (Extended Data Fig. 7e). Forest AGB in the Congo Basin was unrelated to drought (drought:  $\beta = 0.00$ ,  $P = 0.63$ ), even in the most arid regions (Fig. 4e), suggesting that the Congo Basin forests are remarkably resilient to low water availability. These findings align with the higher resilience and positive carbon sink of tropical African forests during strong El Niño droughts<sup>47</sup>, although our results showing the dependence of aridity on temperature suggest that this higher resilience of Congolian forests to water limitation could be at risk in higher temperatures.

The observed increase in AGB with aridity across the Congo Basin—when forests are not thermally limited—alongside a lack of response to stronger droughts (even in the most arid regions) could reflect adaptations or species selection during the marked climatic changes in African forests during the Pleistocene and Holocene<sup>35,48</sup>. A field natural experiment has shown that a shift in species composition in old-growth forests of Ghana with long-term shifts in aridity (lower annual precipitation and longer dry seasons) increased the abundance of non-pioneer tall tree species that are deciduous, drought-tolerant and light-demanding, and resulted in higher forest AGB<sup>1</sup>. Semi-deciduous African forests with intermediate aridity can be more productive than wet evergreen forests, because of high light availability<sup>49</sup>, and tropical African forests can increase their net primary productivity even with an increasing VPD<sup>50</sup>.

We also found that AGB was lower where the storm index was higher across all biogeographical regions, although this association depended on environmental conditions and forest structure (Fig. 3d). High storm index was associated with lower biomass in the Congo Basin ( $\beta = -0.02$ ,  $P = 0.02$ ), where storms are considerably more frequent than they are in other tropical regions (Fig. 1b), as well as in forests experiencing high temperature or aridity across all regions (storm  $\times$   $\ln(\text{MAT})$  in Amazonia:  $\beta = -0.05$ ,  $P < 0.001$ ; storm  $\times$  aridity in the Congo Basin:  $\beta = 0.03$ ,  $P = 0.02$ ; storm  $\times$  aridity in Southeast Asia:  $\beta = -0.15$ ,  $P = 0.03$ ). Storms can reduce forest AGB by damaging and killing trees—lightning can account for as much as 50% of mortality in trees with a diameter at breast height (DBH) greater than 60 cm, and windthrow mortality after blowdowns ranges from 0% to 70%<sup>51,52</sup>. We found that the negative association with storms was stronger under high temperatures or aridity. These results are consistent with field observations showing that physiological stress increases susceptibility to mechanical failure, including stem breakage and uprooting<sup>53,54</sup>.

Our footprint-level analysis for each ecoregion also revealed that the influences of storms were particularly strong in some of the tallest tropical forests (Extended Data Fig. 1). We found that storms had the largest effect size in the eastern Guiana Shield ( $\beta = -0.21$ ,  $P < 0.0001$ ) and a large effect size in Sumatra ( $\beta = -0.09$ ,  $P < 0.001$ ; comparable with the effects of aridity). The eastern Guiana Shield and Southeast Asia experience low frequencies of storms and large-scale wind disturbances<sup>55,56</sup> (Extended Data Fig. 9), which could explain the persistence of trees exceeding 70 m in height, including the tall dipterocarps of Southeast Asia and *Dinizia excelsa* trees in eastern Amazonia<sup>57,58</sup>. Notably, our results show that small increases in storms are associated with disproportionately large reductions in biomass in these forests, making storms one of the strongest—and potentially most underappreciated—controls of the structure and carbon storage of the world's tallest forests.

## Conclusions and future directions

The GEDI spaceborne LiDAR mission mapped forest AGB across the tropics, and thereby provided the power to quantify complex interactions and heterogeneous relationships with climate, soils and topography. The AGB patterns captured in our models reflect broad-scale

interactions between long-term climate, landscape biogeochemistry and natural disturbances such as droughts, heavy rainfall, windthrows and lightning. The spatial association between forest biomass and climate could reflect variation in the functional composition of dominant tree species that shapes the structure and dynamics of tropical forests<sup>59</sup>.

Broadly consistent with previous plot-based evidence of the mechanisms of AGB variation with climate, our findings show that region-specific interactions of climate and other environmental variables result in spatially variable vulnerability of tropical carbon stocks to climatic variability. Considering that temperatures are increasing and dry seasons are becoming longer across some tropical forests<sup>60</sup>, the synergistic effects we have found suggest that the negative effects of temperature and droughts on biomass could be larger than is currently assumed.

The heterogeneous findings also highlight opportunities and avenues for future research. In providing a more comprehensive assessment of the complexity of forest–environment relationships, our work adds nuance to researchers' understanding of forest AGB and its role in the broader planetary system. It calls for targeted field campaigns that are designed to sample environmental gradients in combination rather than in isolation across ecoregions and biogeographical regions, such as the PAN tropical investigation of biogeochemistry and ecological adaptation (PANGAEA) scoping effort<sup>61</sup>. Advancing process-based and Earth system models will require incorporating interaction terms and non-linear responses explicitly, moving beyond additive frameworks to better capture the responses of tropical-forest ecosystems to climate.

## Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-026-10880-2>.

1. Fauset, S. et al. Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecol. Lett.* **15**, 1120–1129 (2012).
2. Lewis, S. L. et al. Above-ground biomass and structure of 260 African tropical forests. *Philos. Trans. R. Soc. B* **368**, 20120295 (2013).
3. Álvarez-Dávila, E. et al. Forest biomass density across large climate gradients in northern South America is related to water availability but not with temperature. *PLoS ONE* **12**, e0171072 (2017).
4. Sullivan, M. J. P. et al. Long-term thermal sensitivity of Earth's tropical forests. *Science* **368**, 869–874 (2020).
5. Muller-Landau, H. C. et al. Patterns and mechanisms of spatial variation in tropical forest productivity, woody residence time, and biomass. *New Phytol.* **229**, 3065–3087 (2021).
6. Shenkin, A. et al. The world's tallest tropical tree in three dimensions. *Front. For. Glob. Change* **2**, 32 (2019).
7. Borges de Lima, R. B. et al. Mapping the density of giant trees in the Amazon. *New Phytol.* **249**, 152–168 (2026).
8. Erb, K.-H. et al. Unexpectedly large impact of forest management and grazing on global vegetation biomass. *Nature* **553**, 73–76 (2018).
9. Johnson, M. O. et al. Variation in stem mortality rates determines patterns of above-ground biomass in Amazonian forests: implications for dynamic global vegetation models. *Glob. Change Biol.* **22**, 3996–4013 (2016).
10. Saatchi, S. S. et al. Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc. Natl Acad. Sci. USA* **108**, 9899–9904 (2011).
11. Mitchard, E. T. A. et al. Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites. *Glob. Ecol. Biogeogr.* **23**, 935–946 (2014).
12. McMichael, C. N. H., Matthews-Bird, F., Farfan-Rios, W. & Feeley, K. J. Ancient human disturbances may be skewing our understanding of Amazonian forests. *Proc. Natl Acad. Sci. USA* **114**, 522–527 (2017).
13. Carvalho, R. L. et al. Pervasive gaps in Amazonian ecological research. *Curr. Biol.* **33**, 3495–3504 (2023).
14. Slik, J. W. F. et al. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics: Large trees and tropical forest biomass. *Glob. Ecol. Biogeogr.* **22**, 1261–1271 (2013).
15. Gora, E. M. et al. Storms are an important driver of change in tropical forests. *Ecol. Lett.* **28**, e70157 (2025).
16. Ramming, A. et al. A generic pixel-to-point comparison for simulated large-scale ecosystem properties and ground-based observations: an example from the Amazon region. *Geosci. Model Dev.* **11**, 5203–5215 (2018).
17. Tavares, J. V. et al. Basin-wide variation in tree hydraulic safety margins predicts the carbon balance of Amazon forests. *Nature* **617**, 111–117 (2023).

18. Chen, S. et al. Amazon forest biogeography predicts resilience and vulnerability to drought. *Nature* **631**, 111–117 (2024).
19. Rowland, L. et al. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* **528**, 119–122 (2015).
20. McDowell, N. et al. Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytol.* **219**, 851–869 (2018).
21. Negrón-Juárez, R. I. et al. Vulnerability of Amazon forests to storm-driven tree mortality. *Environ. Res. Lett.* **13**, 054021 (2018).
22. Gora, E. M., Burchfield, J. C., Muller-Landau, H. C., Bitzer, P. M. & Yanoviak, S. P. Pantropical geography of lightning-caused disturbance and its implications for tropical forests. *Glob. Change Biol.* **26**, 5017–5026 (2020).
23. Feng, Y., Negrón-Juárez, R. I., Romps, D. M. & Chambers, J. Q. Amazon windthrow disturbances are likely to increase with storm frequency under global warming. *Nat. Commun.* **14**, 101 (2023).
24. Guan, K. et al. Photosynthetic seasonality of global tropical forests constrained by hydroclimate. *Nat. Geosci.* **8**, 284–289 (2015).
25. Asner, G. P. et al. Landscape biogeochemistry reflected in shifting distributions of chemical traits in the Amazon forest canopy. *Nat. Geosci.* **8**, 567–573 (2015).
26. Dubayah, R. et al. The Global Ecosystem Dynamics Investigation: high-resolution laser ranging of the Earth's forests and topography. *Sci. Remote Sens.* **1**, 100002 (2020).
27. Potapov, P. et al. Mapping the world's intact forest landscapes by remote sensing. *Ecol. Soc.* **13**, 51 (2008).
28. Duncanson, L. et al. Aboveground biomass density models for NASA's Global Ecosystem Dynamics Investigation (GEDI) lidar mission. *Remote Sens. Environ.* **270**, 112845 (2022).
29. Sullivan, M. J. P. et al. Variation in wood density across South American tropical forests. *Nat. Commun.* **16**, 2351 (2025).
30. Patterson, P. L. et al. Statistical properties of hybrid estimators proposed for GEDI—NASA's global ecosystem dynamics investigation. *Environ. Res. Lett.* **14**, 065007 (2019).
31. Negrón-Juarez, R. et al. Windthrow characteristics and their regional association with rainfall, soil, and surface elevation in the Amazon. *Environ. Res. Lett.* **18**, 014030 (2023).
32. Negrón-Juarez, R. et al. Widespread forest disturbance from windthrow in central African rainforests. *npj Nat. Hazards* **3**, 9 (2026).
33. Chambers, J. Q. et al. Hot droughts in the Amazon provide a window to a future hypertropical climate. *Nature* **649**, 1190–1196 (2026).
34. ter Steege, H. et al. Hyperdominance in the Amazonian tree flora. *Science* **342**, 1243092 (2013).
35. Parmentier, I. et al. The odd man out? Might climate explain the lower tree  $\alpha$ -diversity of African rain forests relative to Amazonian rain forests? *J. Ecol.* **95**, 1058–1071 (2007).
36. Phillips, O. L. et al. Pattern and process in Amazon tree turnover, 1976–2001. *Philos. Trans. R. Soc. B* **359**, 381–407 (2004).
37. Réjou-Méchain, M. et al. Local spatial structure of forest biomass and its consequences for remote sensing of carbon stocks. *Biogeosciences* **11**, 6827–6840 (2014).
38. Phillips, O. L. et al. Drought-mortality relationships for tropical forests. *New Phytol.* **187**, 631–646 (2010).
39. Ashton, P. Dipterocarp biology as a window to the understanding of tropical forest structure. *Annu. Rev. Ecol. Syst.* **19**, 347–370 (1988).
40. Signori-Müller, C. et al. Non-structural carbohydrates mediate seasonal water stress across Amazon forests. *Nat. Commun.* **12**, 2310 (2021).
41. Longo, M. et al. Ecosystem heterogeneity and diversity mitigate Amazon forest resilience to frequent extreme droughts. *New Phytol.* **219**, 914–931 (2018).
42. Bennett, A. C. et al. Sensitivity of South American tropical forests to an extreme climate anomaly. *Nat. Clim. Change* **13**, 967–974 (2023).
43. Aleixo, I. et al. Amazonian rainforest tree mortality driven by climate and functional traits. *Nat. Clim. Change* **9**, 384–388 (2019).
44. Gora, E. M. et al. How some tropical trees benefit from being struck by lightning: evidence for *Dipteryx oleifera* and other large-statured trees. *New Phytol.* **246**, 1554–1566 (2025).
45. Doughty, C. E. et al. Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature* **519**, 78–82 (2015).
46. Aguirre-Gutiérrez, J. et al. Canopy functional trait variation across Earth's tropical forests. *Nature* **641**, 129–136 (2025).
47. Bennett, A. C. et al. Resistance of African tropical forests to an extreme climate anomaly. *Proc. Natl Acad. Sci. USA* **118**, e2003169118 (2021).
48. Réjou-Méchain, M. et al. Unveiling African rainforest composition and vulnerability to global change. *Nature* **593**, 90–94 (2021).
49. Zhang-Zheng, H. et al. Contrasting carbon cycle along tropical forest aridity gradients in West Africa and Amazonia. *Nat. Commun.* **15**, 3158 (2024).
50. Zhao, M. & Running, S. W. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* **329**, 940–943 (2010).
51. Marra, D. M. et al. Large-scale wind disturbances promote tree diversity in a Central Amazon forest. *PLoS ONE* **9**, e103711 (2014).
52. Richards, J. H. et al. Tropical tree species differ in damage and mortality from lightning. *Nat. Plants* **8**, 1007–1013 (2022).
53. Esquivel-Muelbert, A. et al. Tree mode of death and mortality risk factors across Amazon forests. *Nat. Commun.* **11**, 5515 (2020).
54. Reis, S. M. et al. Climate and crown damage drive tree mortality in southern Amazonian edge forests. *J. Ecol.* **110**, 876–888 (2022).
55. Jackson, T. D. et al. Tall Bornean forests experience higher canopy disturbance rates than those in the eastern Amazon or Guiana shield. *Glob. Change Biol.* **30**, e17493 (2024).
56. Negrón-Juarez, R. Widespread windthrow in Southeast Asian tropical forests verified by satellite observations. *Environ. Res. Commun.* **8**, 021003 (2026).
57. Jackson, T. D. et al. The mechanical stability of the world's tallest broadleaf trees. *Biotropica* **53**, 110–120 (2021).
58. de Lima, R. B. et al. Mapping the density of giant trees in the Amazon. *New Phytol.* **249**, 152–168 (2026).
59. Fauset, S. et al. Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun.* **6**, 6857 (2015).
60. Gatti, L. V. et al. Amazonia as a carbon source linked to deforestation and climate change. *Nature* **595**, 388–393 (2021).
61. Ordway, E. M. et al. The PANGAEA Scoping Study Final Report. ORNL DAAC <https://doi.org/10.3334/ORNLDAAC/2405> (2025).
62. Grossiord, C. et al. Plant responses to rising vapor pressure deficit. *New Phytol.* **226**, 1550–1566 (2020).
63. Slot, M., Rifai, S. W., Eze, C. E. & Winter, K. The stomatal response to vapor pressure deficit drives the apparent temperature response of photosynthesis in tropical forests. *New Phytol.* **244**, 1238–1249 (2024).

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## Methods

### GEDI footprints and data filtering

This study used the GEDI L4A estimated AGB product at the footprint level (around 25 m)<sup>64,65</sup> and environmental data to investigate the drivers of AGB across intact lowland forests in the Amazon, the Congo Basin and on the islands of Sumatra and Borneo in Southeast Asia. We used GEDI footprints collected between 1 January and 31 December 2020. We chose that time window to match a map of intact landscapes that had not been disturbed by the end of the year 2020 (<https://glad.umd.edu/intactforests/data.ifl.html>). We first filtered out GEDI footprints that did not meet the requirements for biomass estimation<sup>65</sup>. The quality filter (l4\_quality\_flag = 1), however, does not fully prevent outliers from the presence of persistent cloud coverage, which is frequent in tropical areas; we also removed canopy height values that exceeded 88 m in the Amazon<sup>66</sup>, 82 m in the Congo Basin<sup>67</sup> and 101 m in Southeast Asia<sup>6</sup>.

GEDIL4A biomass models were calibrated using airborne-laser-scanning data to simulate GEDI waveforms over reference biomass plots<sup>28</sup>. These calibrations were developed separately by plant functional type and continent, capturing regional structural and ecological differences. The equations use relative height metrics as predictors, with the 98th height above ground-level percentile (RH98) selected as the sole predictor in most models<sup>28</sup>. Once calibrated, these models are applied to on-orbit GEDI measurements collected from the International Space Station to generate footprint-level biomass predictions along with associated uncertainty estimates. The accuracy of GEDI AGB estimates is intrinsically linked to the quality of GEDI canopy height measurements and the precision of the models used to estimate AGB from ground calibration data<sup>28</sup>. For more information on uncertainties in AGB estimation from GEDI canopy measurements, see Supplementary Methods1. We show the relationships between canopy height and AGB and report the median AGB values (Supplementary Figs. 5 and 6).

We restricted our analyses to intact forests by using a map of intact forest landscapes produced by Global Land Analysis and Discovery (GLAD) to select landscapes that were not disturbed before the end of 2020. An intact forest landscape is defined as a continuous mosaic of forest and naturally treeless ecosystems with no remotely detected signs of human activity that occupies a minimum area of 500 km<sup>2</sup> and is at least 10 km wide at the broadest place<sup>27,68</sup>. We further removed forests that were within 1 km from fragment edges to discard any potential edge effects from land-use change, considering that edge effects affecting biophysical processes that influence forest biomass can extend up to 1 km (ref. 69). The remaining intact forest landscapes comprise 20% of tropical-forest area and 40% of total aboveground tropical-forest carbon<sup>68</sup>. We removed floodplains and wetlands from our analysis using a global land cover and land-use map produced by GLAD in 2019, which was derived from Landsat satellite imagery and topographical data<sup>70</sup>. Such wetlands and floodplains represented around 9% of the GEDI footprints across intact tropical-forest landscapes. They have distinct ecological characteristics, because they are seasonally affected by flooding, which can lead to hypoxic conditions and sediment deposition, shaping species composition, forest structure and dynamics<sup>71,72</sup>.

We also restricted our analysis to lowland areas with a ground elevation between 55 m and 900 m above sea level (ASL) using GEDI's lowest elevation mode product, which is the mean elevation of the centre of the lowest waveform mode relative to the WGS84 reference ellipsoid. By doing this, we removed both coastal vegetation types with an elevation of 55 m or lower, which have direct maritime influences (for example, mangroves, restinga formations)<sup>73,74</sup>, and montane forests at 900 m ASL or higher, which are ecologically distinct and whose forest structure is strongly influenced by cloud dynamics<sup>75–77</sup>. To remove areas under the influences of rock outcrops and other factors that might hamper tree development, we analysed only footprints with a canopy height of at least 5 m on the basis of GEDI's RH98. This also helped remove

sparse and low-stature vegetation that presents higher uncertainties in estimating canopy height with small-size GEDI laser beam footprints<sup>78</sup>.

The resulting range and mean AGB values for each region align with previously published AGB values<sup>79</sup>. The final number of footprints was 13,747,868 for the Amazon, 1,637,208 for the Congo Basin and 397,734 for Southeast Asia, with footprint-level AGB estimates varying from 0 to 1,958 Mg ha<sup>-1</sup>. One of the reasons for the lower number of GEDI shots in Southeast Asia is the persistent cloud coverage in the region relative to other tropical regions. At the footprint level, mean AGB estimates ( $\pm$  s.d.) are  $251 \pm 134$  Mg ha<sup>-1</sup> in the Amazon,  $240 \pm 103$  Mg ha<sup>-1</sup> in the Congo Basin and  $402 \pm 175$  Mg ha<sup>-1</sup> in Southeast Asia (Extended Data Fig. 12). For reference, we also graphed the variation in AGB across intact forest types not included in our analyses—montane forests, mangroves and flooded forests—for each biogeographical region (Supplementary Fig. 2).

We used two complementary approaches to investigate the environmental drivers of AGB across the tropics, using both footprint-level GEDI observations and mean AGB data aggregated to  $2.5 \times 2.5$  km to reduce the measurement noise and sampling uncertainty that are inherent to individual footprints. Footprint-level and aggregated analyses address different ecological questions. Footprint-level data are better for evaluating relationships with environmental drivers that vary at fine scales and for which high-quality data are available at those scales, including topographical variables. At the same time, these data are inherently noisier and have high sampling error, because forests have high stochastic local variation at the footprint scale due to gap-phase dynamics, and thus the aggregated data are better for analysing how mean stand structure and biomass relate to environmental drivers that vary at larger spatial scales. Models are not necessarily comparable, because differences in coefficient magnitude and direction across scales could reflect scale dependence rather than model inconsistency<sup>80</sup>. We therefore present both the footprint-level analysis by ecoregion and the aggregated analysis by biogeographical region (Amazonia, the Congo Basin and Southeast Asia).

### Environmental variables

We at first considered 12 environmental variables that previous studies have associated with spatial variation in tropical-forest tree mortality rates, net primary productivity and/or AGB. Average values of the climatic variables were calculated at the grid-cell level ( $2.5 \times 2.5$  km) as the mean over a time interval ending in December 2019, with start dates varying depending on data availability. The end date for the climate time interval was chosen to ensure that the analysis captured the effects of previous climatic conditions on AGB, because our AGB values are from 2020. We summarize the information for each environmental variable in Extended Data Table 1.

Besides the environmental estimates used in this study, other variables remain to be tested. Differences in geological substrates beyond those captured in our CEC and clay-content estimates could strongly influence AGB through their effects on mineral type, soil age, soil structure, soil depth and access to groundwater<sup>81,82</sup>. Animal occurrence and abundance could have influenced AGB through effects on the density, size and shape of trees<sup>77,83,84</sup>. Other disturbances closely linked to climatic conditions, including strong winds that cause windthrows, wildfires, El Niño–Southern Oscillation events and climate change can affect species and functional composition<sup>85–88</sup>. Although we selected areas without recent human-induced disturbances, AGB in the focal areas could still have been influenced by legacies of human activity in pre-Columbian or post-Columbian societies<sup>89,90</sup>.

MAT and temperature seasonality (annual range in precipitation) were obtained from the WorldClim database of bioclimatic variables at a spatial resolution of 30 arc seconds (often referred to as 1-km spatial resolution)<sup>91</sup>. The WorldClim database was derived from monthly averages of climate as measured at weather stations for the 1950–2000 period and then interpolated using a spline algorithm to create global climate surfaces for monthly precipitation and mean temperature.

# Article

The long-term MAT was calculated from the average yearly temperatures from January 1980 to December 2019. Seasonality in temperature represents the variation in temperature over a year on the basis of the standard deviation of monthly temperature averages.

Drought was assessed using the SPEI, a standardized metric that quantifies deviations in climatic water balance (precipitation minus potential evapotranspiration,  $P - PET$ ) relative to long-term conditions<sup>92</sup>. SPEI integrates precipitation and atmospheric evaporative demand, represented by PET, enabling the assessment of drought severity across multiple timescales. SPEI is calculated by taking the absolute value of the sum of the  $P - PET$  series over a given timescale and standardizing it by fitting a log-logistic probability distribution to a reference period, allowing consistent comparisons across regions, seasons and timescales. We used the Global SPEI database (SPEIbase) v.2.11, available in Google Earth Engine, at 0.5° spatial resolution and monthly temporal resolution<sup>93</sup>. SPEIbase estimates PET using the Penman–Monteith formulation. The SPEI indices were calibrated using the full 1981–2019 reference period. In this study, drought events were defined as periods with  $SPEI < -1$  on a 180-day (6-month) timescale, following a previous study<sup>94</sup>. The 180-day timescale captures short- to medium-term drought conditions, and is ecologically relevant for investigating vegetation responses to prolonged moisture deficits<sup>33,95</sup>. Drought magnitude was quantified as the cumulative SPEI deficit during each event, calculated as the absolute value of the sum of SPEI values below  $-1$  over the duration of the drought. This drought magnitude based on cumulative SPEI integrates both the duration and the intensity of drought conditions into a single measure of total climatic water stress, and does not distinguish short-term from long-term drought events.

MAP, precipitation seasonality, number of months per year with precipitation below 100 mm, number of days per year with precipitation above 20 mm and MCWD were calculated from CHIRPS (Climate Hazards Group Infrared Precipitation with Station) data. CHIRPS integrates satellite imagery with in-situ station data to produce high-resolution estimates of rainfall<sup>96,97</sup>. These variables were calculated using monthly data from January 1981 to December 2019, at a spatial resolution of 0.05° (around 5.6 km). MAP was computed as the long-term average of total annual rainfall, and precipitation seasonality was quantified as the coefficient of variation of monthly precipitation across years, capturing the intra-annual variability in rainfall. MCWD is a measure of aridity within a year, tracking how much precipitation falls short of evapotranspiration in consecutive months. It is an indicator of climatic water stress that does not consider local soil conditions and plant adaptations. We used a global CHIRPS-based MCWD database (<https://zenodo.org/records/4903340>) as in a previous study<sup>96</sup>. MCWD was calculated for each pixel as the negative of the minimum value of accumulated water deficit among all the months in each one of the years.

The number of clear days was computed from Moderate Resolution Imaging Spectroradiometer (MODIS) surface reflectance products at 1,000-m spatial resolution, which provides an estimate of the surface spectral reflectance as it would be measured at ground level in the absence of atmospheric scattering or absorption<sup>98</sup>. We used the Terra MOD09GA v.6 product, which provides an estimate of the surface spectral reflectance of MODIS, corrected for atmospheric conditions. The long-term average was calculated as the mean number of clear days per year at the GEDI footprint level over the period between March 2000 and December 2019.

CAPE was used as an indicator of atmospheric instability and storm potential. In the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5 reanalysis, CAPE is derived from parcel ascent calculations using temperature and humidity profiles, retaining the maximum positive buoyancy among parcels originating below 350 hPa. CAPE represents the vertically integrated excess buoyancy of an air parcel relative to its environment, and is therefore linked to the strength of convective updrafts and the development of intense convective storms. Higher CAPE values indicate environments that are more favourable

for severe convection and associated surface winds. In the Amazon, CAPE has been shown to strongly predict the spatial distribution and density of large windthrow events, with windthrows occurring nearly eight times more frequently in environments where CAPE exceeds  $1,023 \text{ J kg}^{-1}$  than in lower-CAPE environments<sup>23</sup>. Storm-generated winds cause tree mortality through uprooting, often mediated by soil properties, and stem breakage associated with mechanical failure<sup>21</sup>. We used afternoon mean CAPE values averaged from hourly ERA5 data from 17:00 and 23:00 UTC in local time over 1980–2019, following a previous study<sup>23</sup>. These average CAPE values over 40 years can capture the spatial pattern in CAPE while minimizing the influence of interannual climate variability on windthrow occurrence<sup>23</sup>. Our focal regions are outside the cyclone belts, and thus never experience cyclonic storms. In regions where they occur, cyclones (known in some regions as hurricanes) have large and pervasive effects on forest structure, by killing and damaging trees<sup>99</sup>. Lightning stroke density (strokes per km per month) was calculated from georeferenced stroke-count data from the World Wide Lightning Location Network (<https://zenodo.org/records/10725446>), gridded at 0.5° resolution and hourly temporal resolution. The long-term average lightning stroke density was then calculated as the mean value at the GEDI footprint level over the period between Jan 2010 and December 2019.

Soil CEC in  $\text{cmol}_c \text{ kg}^{-1}$  at 15-cm depth and soil clay content at 30-cm depth were predicted using a global compilation of soil ground observations at 250-m resolution<sup>100</sup>. Soil clay content was obtained using OpenLandMap and soil CEC was obtained from the International Soil Reference and Information Centre (ISRIC)'s SoilGrids (<https://data.isric.org/geonetwork/srv/api/records/5333b1af-7620-407f-8bca-2303fc5c7288>)<sup>100</sup>. Predictions were based on approximately 150,000 soil profiles used for training and a stack of 158 remote sensing-based soil covariates (derived mainly from MODIS land products, Shuttle Radar Topography Mission (SRTM) digital elevation model derivatives, climatic images and global landform and lithology maps), which were used to fit an ensemble of machine-learning methods.

Topographical variation spans multiple spatial scales, from centimetre-scale surface roughness to mountain systems extending hundreds of kilometres. As a result, the links between tropical forest structure and topographical metrics depend on the spatial scale at which those metrics are derived<sup>101</sup>. We used slope at a 30-m scale, as well as TPI at both 150-m and 1,000-m scales, as topographical variables that together are associated with plateaus, slopes, valleys, hilltops, ridges and drainage systems<sup>25,101–103</sup>. Slope quantifies the steepness of the terrain and affects water, nutrients and light availability<sup>102</sup>, and was calculated from the 30-m SRTM digital elevation model as the maximum rate of elevation change between each pixel and its surrounding neighbours, expressed in degrees. TPI describes the height of a pixel relative to the surrounding landscape and ranges from negative where the terrain is concave (valleys) to positive where it is convex (ridges and hilltops). TPI was calculated using the global NASA SRTM as input (30 m) by subtracting the mean elevation of a local neighbourhood from the original elevation value at each pixel using a moving window (kernel search), essentially comparing each pixel's elevation to its surrounding area. TPI was computed at two neighbourhood scales: a microscale TPI of 150 m (around 5 pixels), capturing fine-scale topographical variation such as small local ridges and small depressions (for example, *baixios*), which are linked to local patterns of water redistribution, nutrient mobility and resource accumulation; and a mesoscale TPI of 1 km (around 33 pixels), capturing intermediate landform positions including hills, valley systems and drainage features that are associated with variation in biomass across the landscape<sup>25,101</sup>.

## Statistical analysis

AGB was modelled separately for each biogeographical region (Amazonia, Congo Basin and Southeast Asia) as a function of all environmental variables listed in Extended Data Table 1. Models were fitted separately

for each biogeographical region to account for region-specific relationships between AGB and environmental drivers. Fitting separate models allowed each region to be modelled without forcing a one-size-fits-all effect that might not hold everywhere, and also allowed region-specific interactions that might not be meaningful globally. Amazon forests were subdivided into six ecoregions (Fig. 1a): southwestern Amazon, northwestern Amazon, central Amazon, the eastern and western Guiana Shields and the southern Amazon), following a previous study<sup>34</sup>. The Congo Basin was subdivided into five ecoregions: Atlantic equatorial coastal Congolian, northwestern Congolian, Congolian swamps, central Congolian and northeastern Congolian forest, following a previous study<sup>104</sup>. Southeast Asian forests were subdivided into two ecoregions—Sumatra and Borneo—following the same previous study<sup>104</sup>.

Some of the climatic variables that could affect AGB strongly co-varied (Supplementary Fig. 1) and could have intertwined effects on AGB that are difficult to separate. For example, higher MAP across the Amazon can be linked to heavy rains with daily precipitation higher than 20 mm. We thus used a PCA to reduce the climatic variables into a single dimension of climatic variability. This approach reduces the influence of collinearity in regression analysis. We specifically included ten variables in the PCA: MCWD, MAP, MAT, number of months per year with precipitation  $\leq 100$  mm, number of days per year with precipitation  $\geq 20$  mm, number of clear days per year, precipitation seasonality, temperature seasonality, zonal wind speed and lightning stroke density. We found a dominant axis capturing the climatic seasonality marked by water deficit and direct solar radiation (Extended Data Fig. 2a), which we refer to as the drought axis. Lightning and CAPE were also strongly related and therefore we created an index using a PCA that accounts for both lightning and CAPE values that are related to windthrows. Specifically, we derived a convective storm index by combining excess CAPE above a physically meaningful threshold for deep convection ( $1,023 \text{ J kg}^{-1}$ ) with lightning frequency. CAPE values below this threshold have lower windthrow relevance, whereas values above it increase storm destructiveness nonlinearly with an eight times higher probability of windthrows<sup>23</sup>. We therefore squared and tripled the excess CAPE (CAPE<sup>2</sup> and CAPE<sup>3</sup>) term to amplify extreme values and performed a PCA on these variables and lightning frequency; the first principal component explained 76% of the variance and was used as an integrated predictor of storm intensity in all models (Extended Data Fig. 2b).

To analyse AGB at regional scales while accounting for fine- and coarse-scale environmental drivers, we aggregated footprint-level GEDI observations to 2.5-km pixels by computing the mean AGB and associated sample size per pixel. Coarse-resolution environmental predictors (temperature, aridity, SPEI, storms, CEC and clay content) were assigned to each pixel from the source rasters, and topographical variables derived at high resolution (TPI and slope) were summarized as pixel mean values. Because topographical variables were at finer spatial resolution than climatic variables were, we quantified variance before and after aggregation to evaluate the degree of information loss and shifts in median values with aggregation (Supplementary Fig. 3). Aggregating TPI could mask fine-scale topographical variability, but still captures broad-scale patterns in topography, reflecting whether an area is plateau-like, or dominated by valleys and small depressions or hilltops.

We developed separate LME models to predict AGB for each biogeographical region (or ecoregion when using footprint-level GEDI data) as a function of environmental predictors included as additive terms. Predictors included non-collinear climatic variables (aridity axis, MAT, drought magnitude based on cumulative SPEI deficit, and storms), edaphic variables (CEC and soil clay content), and topographical variables (slope and TPI at 150 m and 1,000 m spatial scales). To capture potential nonlinearities, we tested log-transformed and quadratic terms for each predictor, as well as interaction terms to investigate the conditional dependency of one variable on another. All predictors and AGB were centred within each tropical region and scaled using the

global standard deviation calculated across all regions. This allows the standardized coefficients to be comparable across regions, even though the models were fitted separately for each biogeographical region. Therefore, differences in effect sizes reflect the relative importance of environmental drivers on a global scale, while capturing within-region variation. This global standardization ensures that differences in standardized coefficients reflect the relative ecological importance of each driver rather than differences in covariate ranges or distributions within regions. Models were fitted using the lme function in the nlme R package.

At the aggregated data level, the LME models included random effects for spatial location, specifically for grid cells within a fine spatial grid nested within ecoregion, to account for spatial autocorrelation and other influencing factors, including species and functional composition<sup>34</sup>. To account for spatial autocorrelation, we implemented a nested random-effect structure, with sampling units grouped into 50 km  $\times$  50-km grids nested within ecoregions. This choice was guided by the observation that smaller grid cells at the 2.5-km-pixel scale could absorb fine-scale variance in predictors, artificially reducing effect sizes. By using larger 50-km grid cells, the models captured broad-scale spatial autocorrelation while allowing fixed effects to explain the fine-scale variation in AGB. Weights proportional to the log-transformed number of GEDI footprints per pixel were applied through the varFixed function to account for differences in sampling precision, giving greater influence to pixels with more observations. We present the methods related to footprint-level analysis by ecoregion in Supplementary Methods 8 and the results in Extended Data Fig. 1.

Because the number of possible interactions was very large, we used a two-step approach to focus on the most important terms. We tested all variables and interaction terms using LASSO, a method that identifies which interactions help explain variation in the residuals of the random-effects model. Interactions that were identified as non-important by LASSO and also had  $P > 0.05$  in the full model were excluded, and all main effects were retained. We then treated variance inflation factors (VIFs) as a diagnostic of collinearity, and kept ecologically justified interactions with VIF values up to 10 when effect directions were stable and supported by LASSO.

For the final aggregated data-based LME models, we calculated the marginal  $R^2$ , which can be interpreted as the variance explained by all fixed effects in the model, as well as the conditional  $R^2$ , which estimates the variance explained by fixed (environmental variables) and random (spatial grid of 50  $\times$  50 km and ecoregion) effects combined. We compared the  $R^2$  values of LME and random forest models as a complementary analysis to test whether model uncertainties arise from non-linear relationships and complex interactions that are difficult to specify in LME but can be captured by random forests (Supplementary Table 6).

## Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

The data supporting the findings of this study are publicly available via Zenodo at <https://doi.org/10.5281/zenodo.19474558> (ref. 105). Version 1 contains forest structure and environmental data at the GEDI footprint level, whereas version 2 contains forest structure and environmental data aggregated to 2.5  $\times$  2.5-km grid cells. Source datasets used in this study are publicly available and include NASA GEDI Level 4A AGB density data (<https://doi.org/10.3334/ORNLDAAC/2056>), WorldClim climate data (<https://worldclim.org/data/worldclim21.html>), the Global SPEI database (SPEIbase v.2.10 (Earth Engine Data Catalog and Google for Developers)), CHIRPS precipitation data (<https://www.chc.ucsb.edu/data/chirps>), the CHIRPS-derived MCWD dataset (<https://doi.org/10.5281/zenodo.4903340>), MODIS MOD09GA version 6 surface

reflectance data (<https://lpdaac.usgs.gov/products/mod09gav061/>), ERA5 reanalysis data (<https://cds.climate.copernicus.eu/datasets/reanalysis-era5-single-levels>), World Wide Lightning Location Network lightning data (<https://doi.org/10.5281/zenodo.10725446>), SoilGrids soil data (<https://soilgrids.org>), OpenLandMap soil data (<https://openlandmap.org>), SRTM elevation data from NASA Earthdata (<https://earthdata.nasa.gov>) and GLAD intact forest landscapes and global land cover datasets (<https://glad.umd.edu>). All processed data required to reproduce the analyses are available in the Zenodo repository.

## Code availability

Custom R scripts used for data processing, statistical analyses and figure generation are publicly available via Zenodo at <https://doi.org/10.5281/zenodo.19474558> (ref. 105).

64. Dubayah, R. O. et al. GEDI L3 Gridded Land Surface Metrics, version 1. ORNL DAAC <https://doi.org/10.3334/ORNLDAAAC/1865> (2021).
65. Kellner, J. R., Armston, J. & Duncanson, L. Algorithm theoretical basis document for GEDI footprint aboveground biomass density. *Earth Space Sci.* **10**, e2022EA002516 (2023).
66. Gorgens, E. B. et al. The giant trees of the Amazon basin. *Front. Ecol. Environ.* **17**, 373–374 (2019).
67. Hemp, A. et al. Africa's highest mountain harbours Africa's tallest trees. *Biodivers. Conserv.* **26**, 103–113 (2017).
68. Potapov, P. et al. The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013. *Sci. Adv.* **3**, e1600821 (2017).
69. Laurance, W. F. et al. An Amazonian rainforest and its fragments as a laboratory of global change: Amazonian fragments and global change. *Biol. Rev. Camb. Philos. Soc.* **93**, 223–247 (2018).
70. Hansen, M. C. et al. Global land use extent and dispersion within natural land cover using Landsat data. *Environ. Res. Lett.* **17**, 034050 (2022).
71. Householder, J. E. et al. Modeling the ecological responses of tree species to the flood pulse of the Amazon Negro River floodplains. *Front. Ecol. Evol.* **9**, 628606 (2021).
72. Householder, J. E. et al. One sixth of Amazonian tree diversity is dependent on river floodplains. *Nat. Ecol. Evol.* **8**, 901–911 (2024).
73. Rovai, A. S. et al. Scaling mangrove aboveground biomass from site-level to continental-scale: scaling up mangrove AGB from site- to continental-level. *Glob. Ecol. Biogeogr.* **25**, 286–298 (2016).
74. Simard, M. et al. Mangrove canopy height globally related to precipitation, temperature and cyclone frequency. *Nat. Geosci.* **12**, 40–45 (2019).
75. Corlett, R. T. & Primack, R. B. *Tropical Rain Forests: an Ecological and Biogeographical Comparison* (Wiley-Blackwell, 2011).
76. Oliveira, R. S., Eller, C. B., Bittencourt, P. R. L. & Mulligan, M. The hydroclimatic and ecophysiological basis of cloud forest distributions under current and projected climates. *Ann. Bot.* **113**, 909–920 (2014).
77. Cuni-Sanchez, A. et al. High aboveground carbon stock of African tropical montane forests. *Nature* **596**, 536–542 (2021).
78. Pascual, A. et al. Assessing the performance of NASA's GEDI L4A footprint aboveground biomass density models using National Forest Inventory and airborne laser scanning data in Mediterranean forest ecosystems. *For. Ecol. Manage.* **538**, 120975 (2023).
79. Avitabile, V. et al. An integrated pan-tropical biomass map using multiple reference datasets. *Glob. Change Biol.* **22**, 1406–1420 (2016).
80. Takyu, M., Aiba, S.-I. & Kitayama, K. Changes in biomass, productivity and decomposition along topographical gradients under different geological conditions in tropical lower montane forests on Mount Kinabalu, Borneo. *Oecologia* **134**, 397–404 (2003).
81. Asner, G. P., Flint Hughes, R., Varga, T. A., Knapp, D. E. & Kennedy-Bowdoin, T. Environmental and biotic controls over aboveground biomass throughout a tropical Rain Forest. *Ecosystems* **12**, 261–278 (2009).
82. Berzaghi, F. et al. Carbon stocks in central African forests enhanced by elephant disturbance. *Nat. Geosci.* **12**, 725–729 (2019).
83. Sorokina, H. E. et al. East African megafauna influence on vegetation structure permeates from landscape to tree level scales. *Ecol. Inform.* **79**, 102435 (2024).
84. Magnabosco Marra, D. et al. Windthrows control biomass patterns and functional composition of Amazon forests. *Glob. Change Biol.* **24**, 5867–5881 (2018).
85. Nogueira, D. S. et al. Impacts of fire on forest biomass dynamics at the southern Amazon edge. *Environ. Conserv.* **46**, 285–292 (2019).

86. Berenguer, E. et al. Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. *Proc. Natl Acad. Sci. USA* **118**, e2019377118 (2021).
87. Aguirre-Gutiérrez, J. et al. Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity. *Nat. Commun.* **11**, 3346 (2020).
88. Levis, C. et al. Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* **355**, 925–931 (2017).
89. Oliveira, E. A. et al. Legacy of Amazonian Dark Earth soils on forest structure and species composition. *Glob. Ecol. Biogeogr.* **29**, 1458–1473 (2020).
90. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
91. Vicente-Serrano, S. M., Beguería, S. & López-Moreno, J. I. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J. Clim.* **23**, 1696–1718 (2010).
92. Beguería, S., Vicente Serrano, S. M., Reig-Gracia, F. & Latorre Garcés, B. SPEIbase v.2.9 [Dataset]. *DIGITAL.CSIC* <https://doi.org/10.20350/DIGITALCSIC/15470> (2023).
93. Gebrechorkos, S. H. et al. Warming accelerates global drought severity. *Nature* **642**, 628–635 (2025).
94. Zhong, S., Sun, Z. & Di, L. Characteristics of vegetation response to drought in the CONUS based on long-term remote sensing and meteorological data. *Ecol. Indic.* **127**, 107767 (2021).
95. Aragão, L. E. O. C. et al. Spatial patterns and fire response of recent Amazonian droughts. *Geophys. Res. Lett.* **34**, L07701 (2007).
96. Funk, C. et al. The climate hazards infrared precipitation with stations—a new environmental record for monitoring extremes. *Sci. Data* **2**, 150066 (2015).
97. Kang, S., Running, S. W., Zhao, M., Kimball, J. S. & Glassy, J. Improving continuity of MODIS terrestrial photosynthesis products using an interpolation scheme for cloudy pixels. *Int. J. Remote Sens.* **26**, 1659–1676 (2005).
98. Uriarte, M., Thompson, J. & Zimmerman, J. K. Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. *Nat. Commun.* **10**, 1362 (2019).
99. Hengl, T. et al. SoilGrids250m: global gridded soil information based on machine learning. *PLoS ONE* **12**, e0169748 (2017).
100. Detto, M., Muller-Landau, H. C., Mascaro, J. & Asner, G. P. Hydrological networks and associated topographic variation as templates for the spatial organization of tropical forest vegetation. *PLoS ONE* **8**, e76296 (2013).
101. Mascaro, J. et al. Controls over aboveground forest carbon density on Barro Colorado Island, Panama. *Biogeosciences* **8**, 1615–1629 (2011).
102. Jucker, T. et al. Topography shapes the structure, composition and function of tropical forest landscapes. *Ecol. Lett.* **21**, 989–1000 (2018).
103. Dinerstein, E. et al. An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* **67**, 534–545 (2017).
104. Levin, S. A. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. *Ecology* **73**, 1943–1967 (1992).
105. Nunes, M. H. GEDI data of lowland intact tropical forests. *Zenodo* <https://doi.org/10.5281/zenodo.19474558> (2026).

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**Author contributions** Conceptualization: M.H.N. Methodology: M.H.N., H.C.M.-L., E.B.G., A.P. and R.D. Investigation: M.H.N. and H.C.M.-L. Visualization: M.H.N. Funding acquisition: R.D. Writing (original draft): M.H.N. Writing (review and editing): M.H.N., H.C.M.-L., E.B.G., A.P. and R.D.

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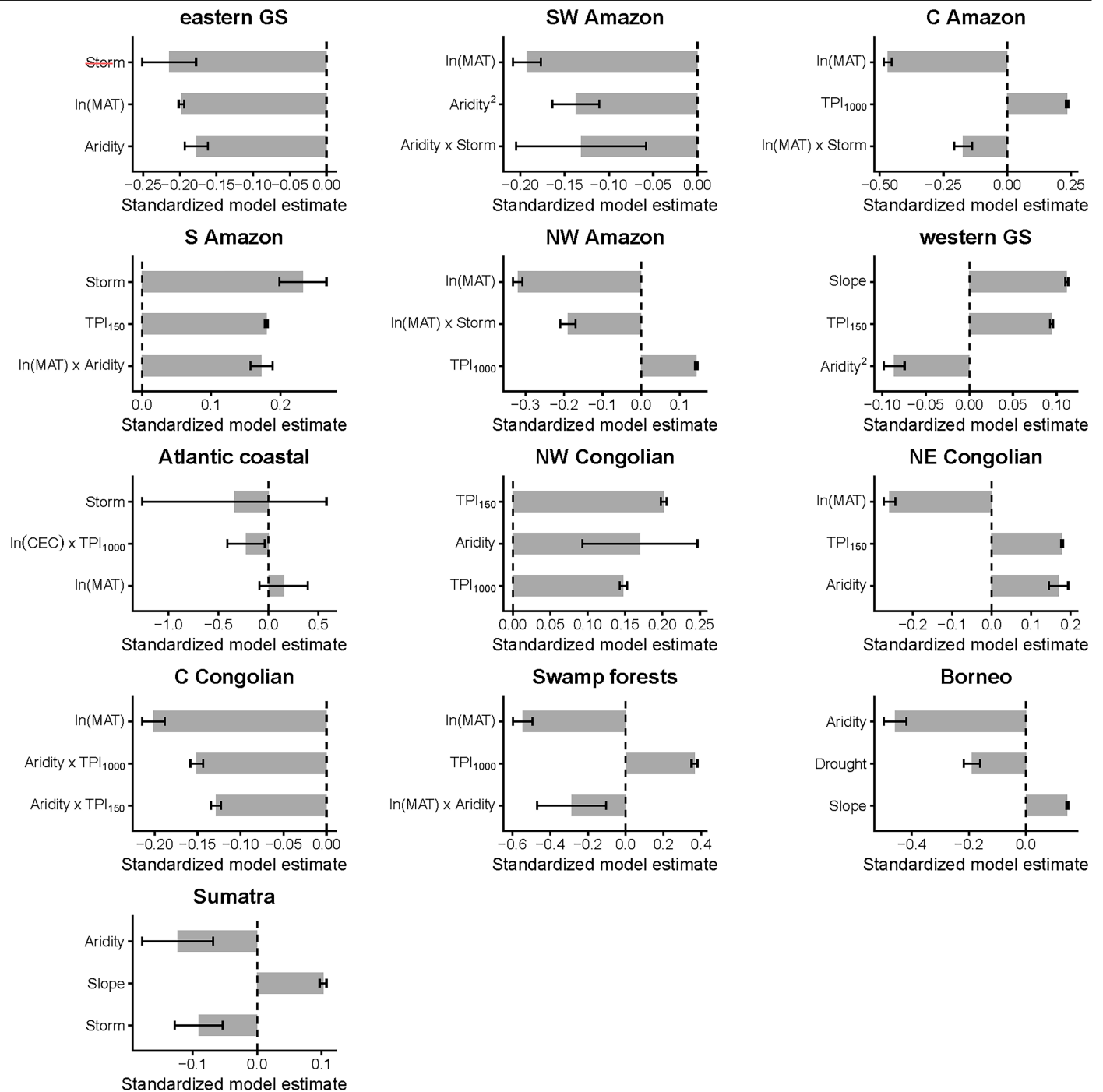
## Additional information

**Supplementary information** The online version contains supplementary material available at <https://doi.org/10.1038/s41586-026-10880-2>.

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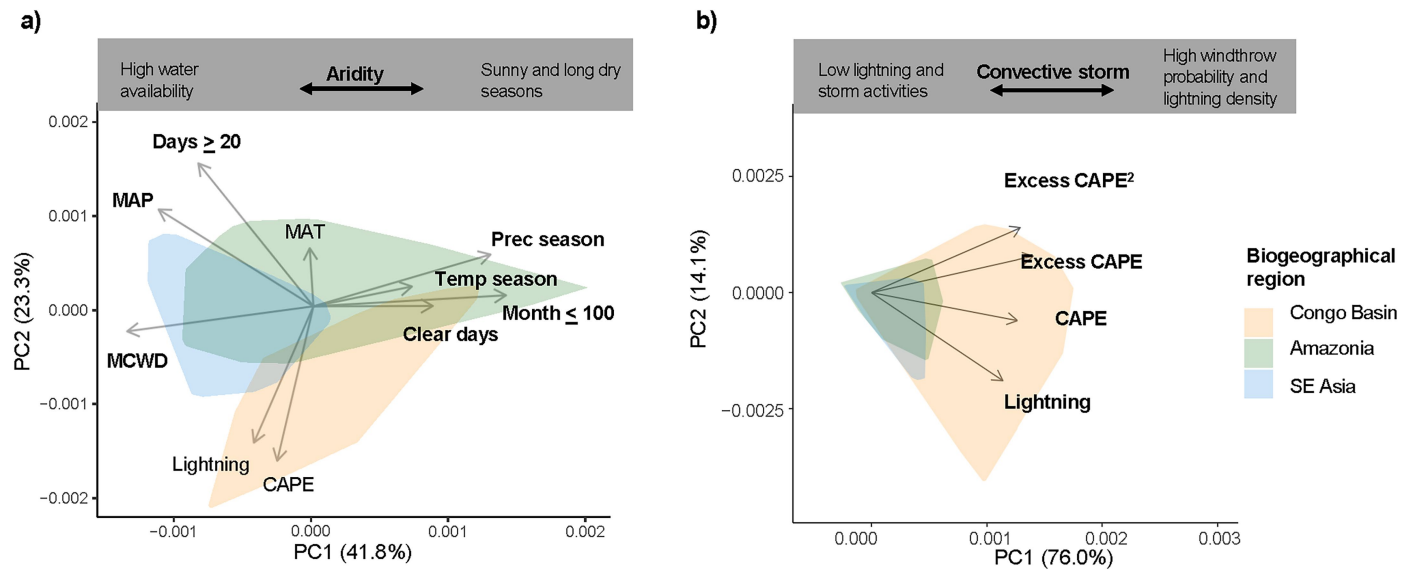
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**Extended Data Fig. 1 | Separate LME models for each ecoregion based on footprint-level GEDI data.** Standardized estimates (global scaling, ecoregional centring) of the top 3 most influential environmental variables based on their coefficient values based on LME models for each ecoregion. LME models incorporated climatic (aridity, drought, MAT and storm), soil (clay content and CEC), and topographical (TPI at 150 and 1,000 m, and slope) predictors, along with their interactions. LME models specified a  $10 \times 10$  km spatial grid as random effect to account for spatial autocorrelation. Values to the left of the zero line indicate negative model estimates, and those to the

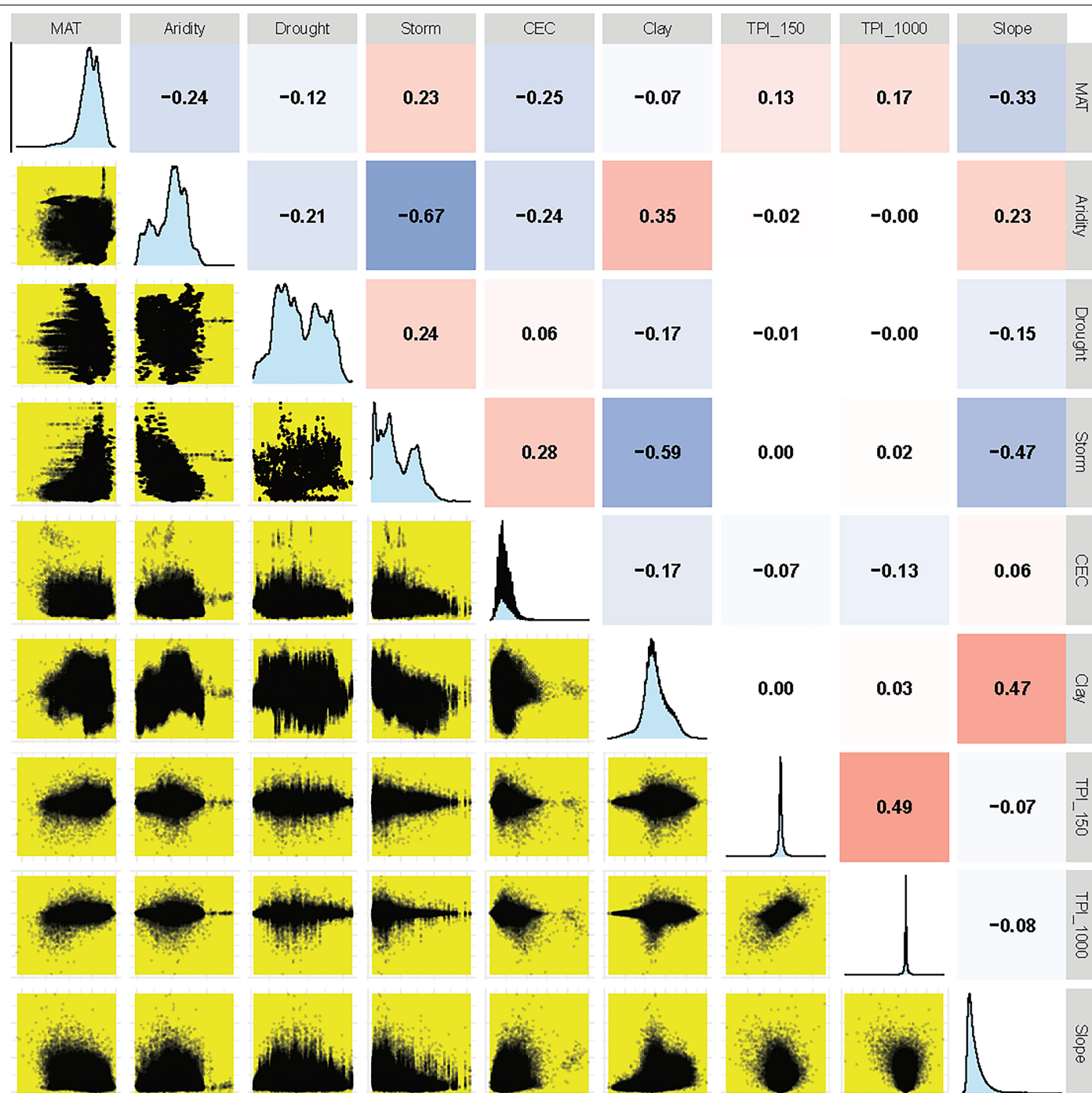
right indicate positive estimates. Sample sizes: Amazon  $n \approx 13,747,868$ ; Congo Basin  $n \approx 1,637,208$ ; Southeast Asia  $n \approx 397,734$  footprints. Error bars represent mean  $\pm$  95% confidence intervals. We show one panel for each ecoregion, considering six ecoregions in Amazonia (Northwestern Amazon, Southwestern Amazon, Western Guiana Shield, Central Amazon, eastern Guiana Shield and Southern Amazon), five ecoregions in the Congo Basin (Atlantic coastal forests, Northwestern Congolian, Swamp forests, Central Congolian and Northeastern Congolian), and two in Southeast Asia (Sumatra and Borneo).





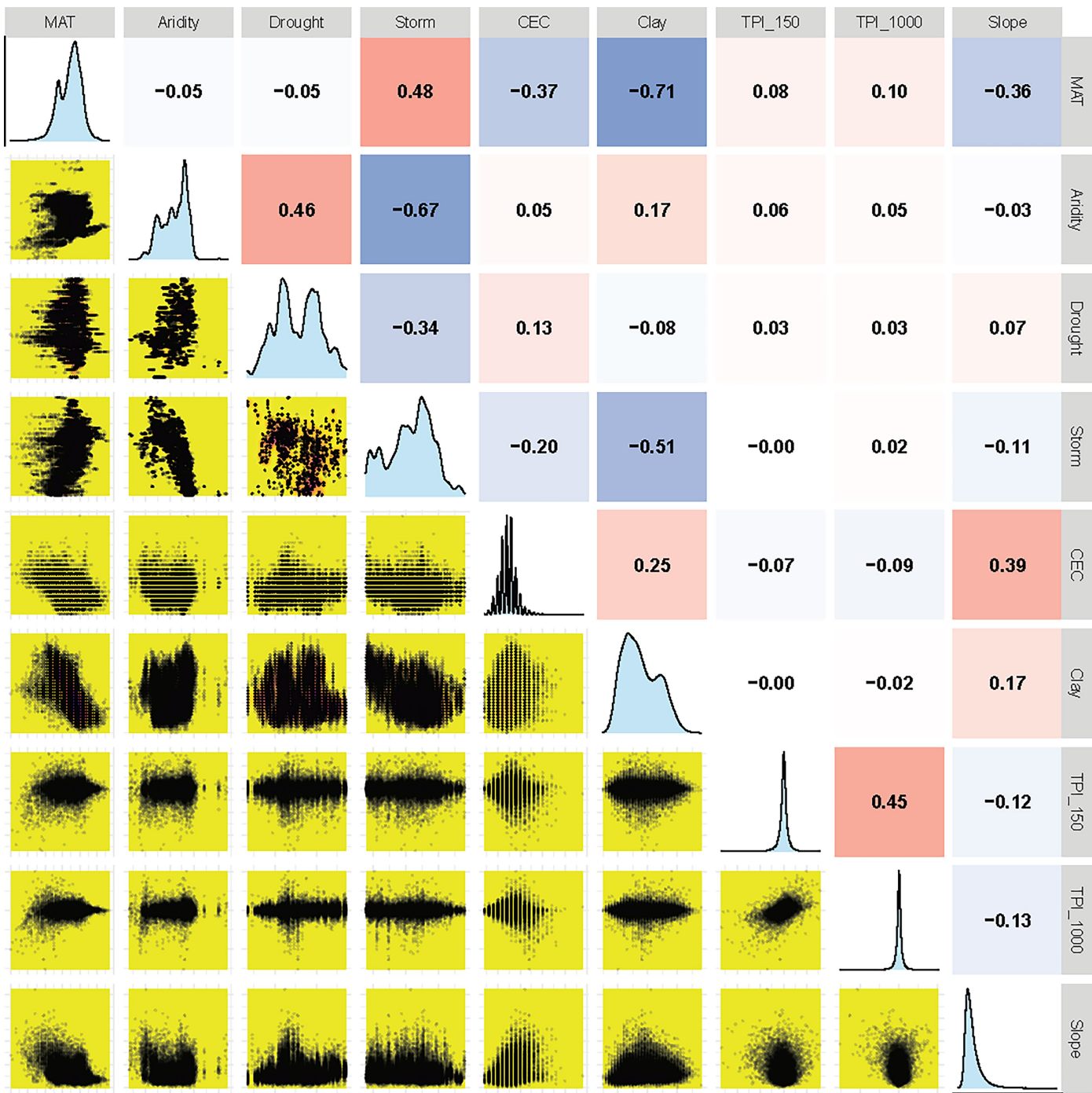
**Extended Data Fig. 2 | Aridity and storm indices derived from separate PCAs.** PCA with the three biogeographical regions (Amazon, Congo Basin and Southeast Asia) combined shows that: **a)** one main axis of variation corresponds to aridity, with low values corresponding to high water availability and high values corresponding to prolonged dry seasons with clear skies. The shaded areas correspond to the climatic envelope based on 10 climatic variables, namely, MAT, MAP, N° days  $\geq 20$  mm year<sup>-1</sup>, MCWD, lightning, CAPE, N° months  $\leq 100$  mm year<sup>-1</sup>, temperature seasonality, precipitation seasonality and N° of clear days. MCWD has negative values, with the highest value as 0. It takes value 0 in everwet forests in which precipitation exceeds potential evapotranspiration in every month of the year. Thus, higher MCWD values correspond to wetter conditions. Bold names indicate variables that had a

higher contribution to the aridity axis, whereas the other variables did not contribute to this aridity dimension (MAT, lightning and CAPE); **b)** another main axis of variation corresponds to convective storms, with low values corresponding to low storm intensity and lightning density, and high values corresponding to high probability of windthrow and lightning density. We also included first- and second-order excess CAPE variables, defined as CAPE values above 1023 J kg<sup>-1</sup>, with values below this threshold set to zero, to account for disproportionately high CAPE values that have a high probability of windthrows. The shaded areas correspond to the storm index based on lightning density and CAPE. Climatic variables at the aggregated level were used for both PCAs, with sample sizes as: Amazon n  $\approx$  216,667; Congo Basin n  $\approx$  40,306; Southeast Asia n  $\approx$  29,436.



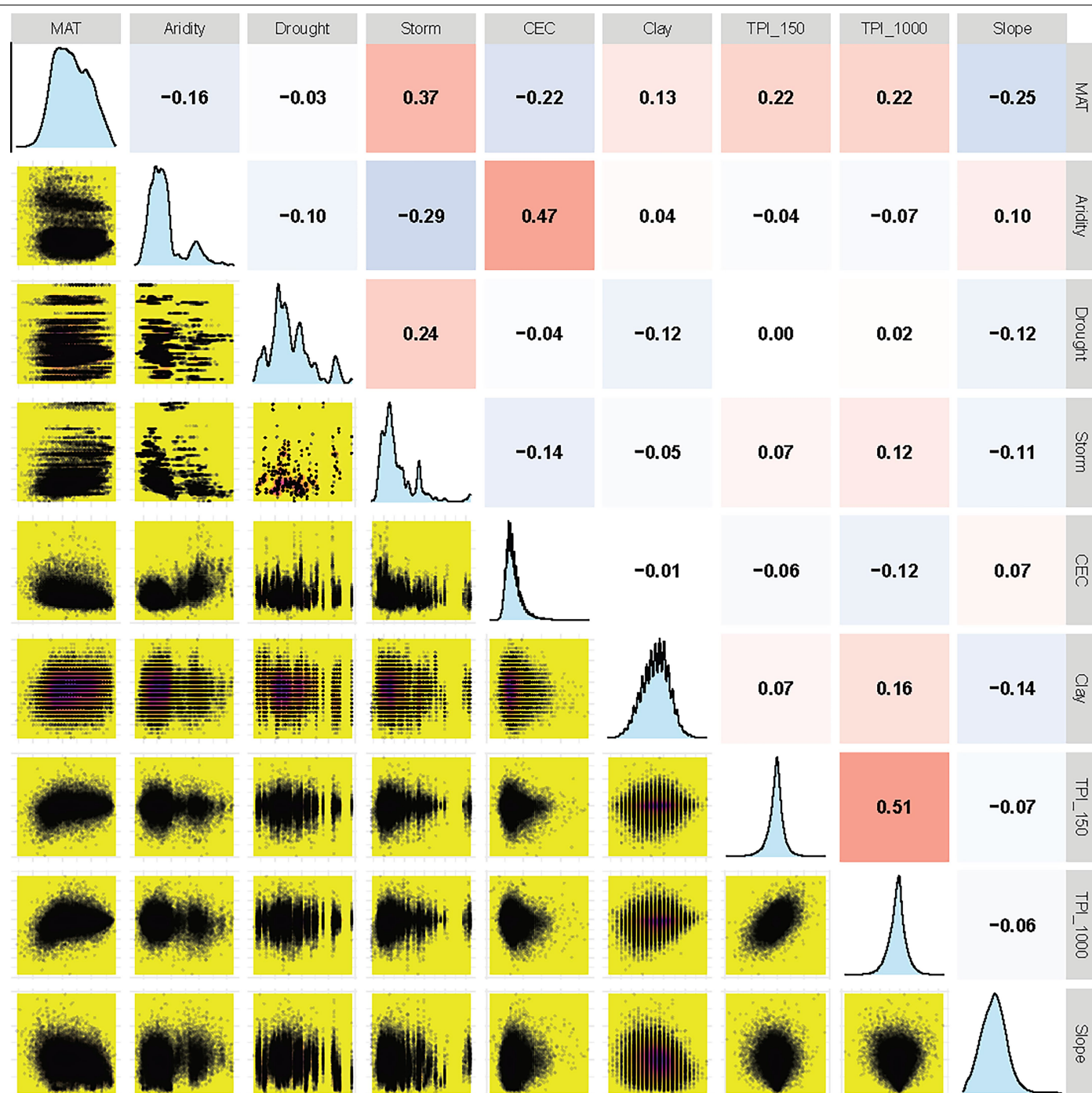
**Extended Data Fig. 3 | Correlation analysis among independent climatic, soil and topographical variables in the Amazon.** Environmental variables are MAT, the aridity index from PCA, drought calculated from SPEI, the storm index also from PCA, CEC, soil clay content (Clay), TPI in two scales, 150 and 1,000 m,

as well as slope. Colour and shade intensity reflect the direction and magnitude of the correlation. The pairwise scatter plots in the lower triangle correspond to the relationship between individual environmental variables. Sample sizes: Amazon  $n \approx 216,667$ .



**Extended Data Fig. 4 | Correlation analysis among independent climatic, soil and topographical variables in the Congo Basin.** Environmental variables are MAT, the aridity index from PCA, drought calculated from SPEI, the storm index also from PCA, CEC, soil clay content (Clay), TPI in two scales,

150 and 1,000 m, as well as slope. Colour and shade intensity reflect the direction and magnitude of the correlation. The pairwise scatter plots in the lower triangle correspond to the relationship between individual environmental variables. Sample sizes: Congo Basin  $n \approx 40,306$ .

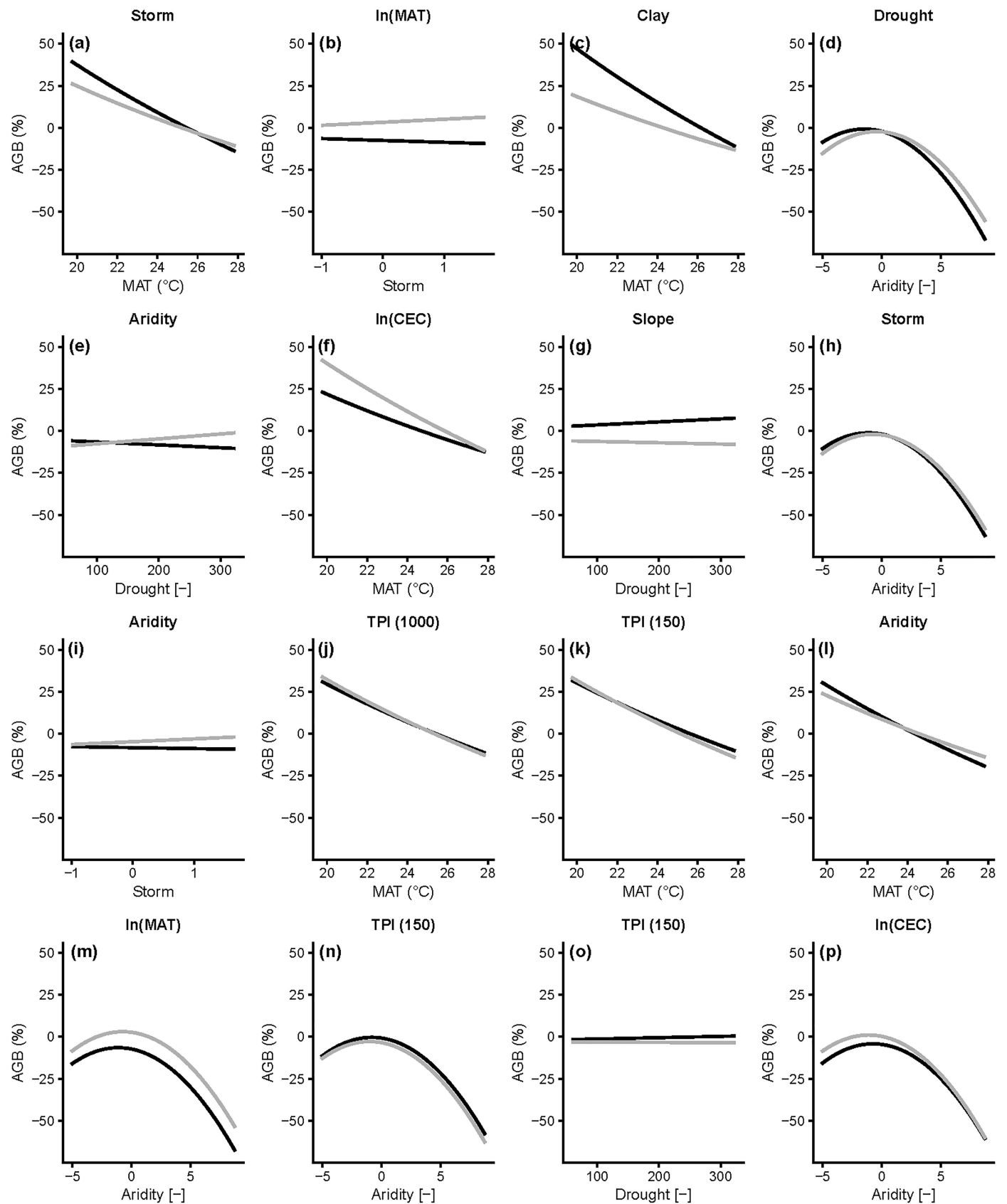


**Extended Data Fig. 5 | Correlation analysis among independent climatic, soil and topographical variables in Southeast Asia.** Environmental variables are MAT, the aridity index from PCA, drought calculated from SPEI, the storm index also from PCA, CEC, soil clay content (Clay), TPI in two scales, 150 and

1,000 m, as well as slope. Colour and shade intensity reflect the direction and magnitude of the correlation. The pairwise scatter plots in the lower triangle correspond to the relationship between individual environmental variables. Sample sizes: Southeast Asia  $n \approx 29,436$ .



## Amazonia



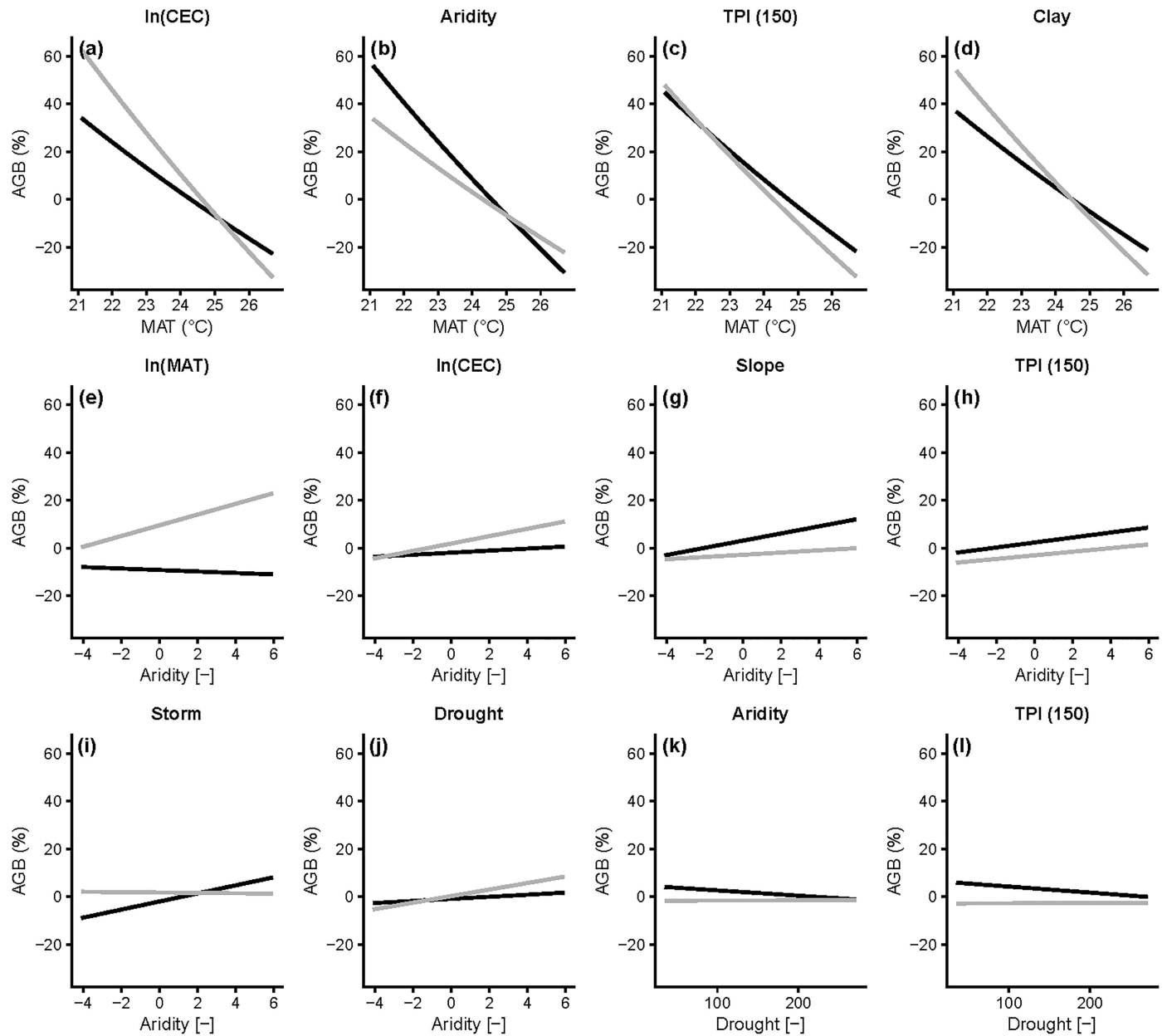
Extended Data Fig. 6 | See next page for caption.

**Extended Data Fig. 6 | Effects of interactions between environmental variables on predicted AGB, relative to the regional mean AGB, in the Amazon.** Grey lines are the 10% lowest quantile and black curves are the 90% highest quantile of the variable displayed in the title (representing the modifier variable) interacting with the x-axis variable. We show the effects of a) ln(MAT) with storms; b) storms with ln(MAT); c) ln(MAT) with soil clay content; d) aridity

with drought; e) drought with aridity; f) ln(MAT) with soil CEC; g) drought with slope; h) aridity with storms; i) storms with aridity; j) ln(MAT) with TPI (1000); k) ln(MAT) with TPI (150); l) ln(MAT) with aridity; m) aridity with ln(MAT); n) aridity with TPI at 150 m scale; o) drought with TPI at 150 m scale; and p) aridity with soil CEC. Sample size = 216,667. Predictions were based on LME models.



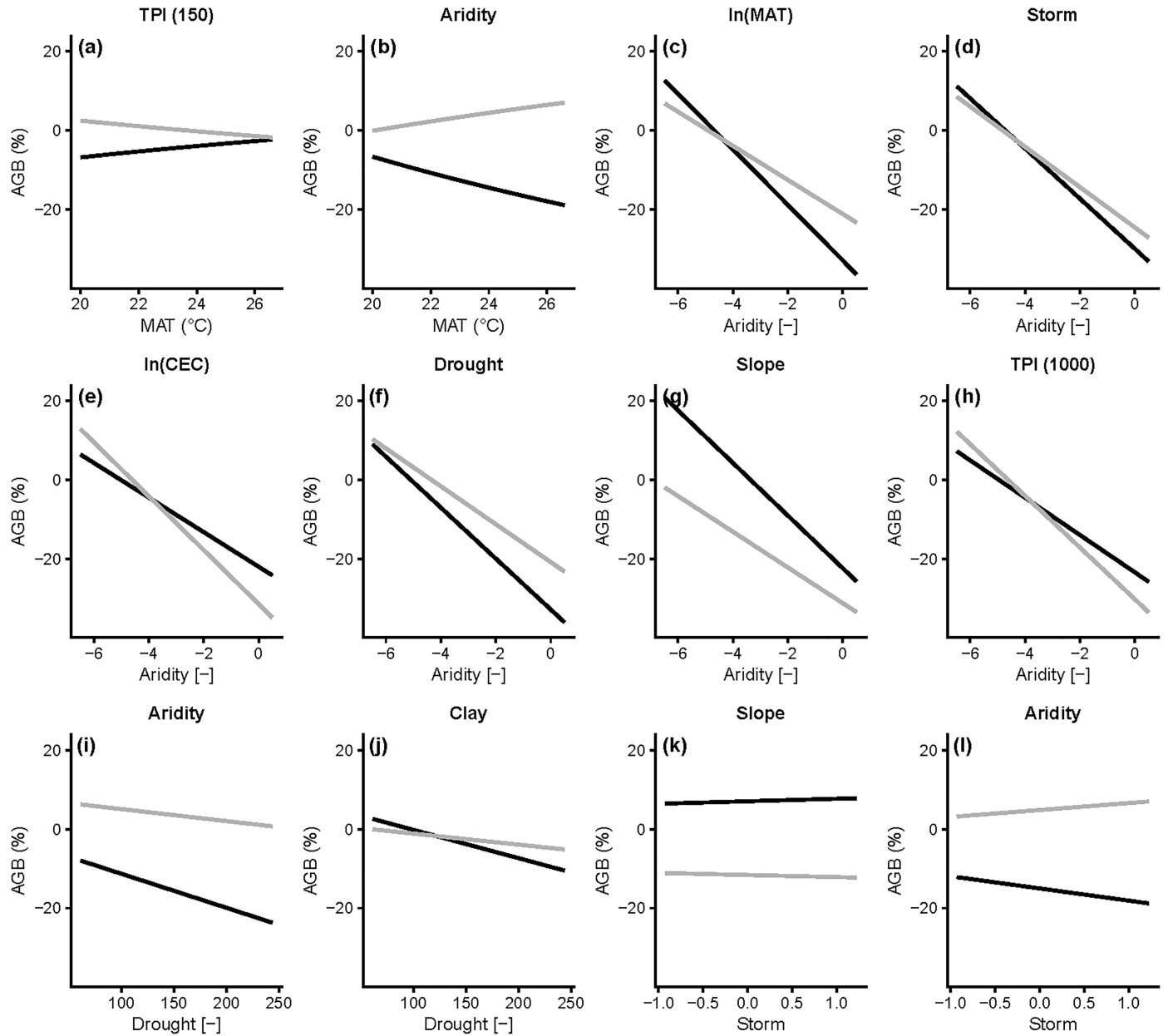
## Congo Basin



**Extended Data Fig. 7 | Effects of interactions between environmental variables on predicted AGB, relative to the regional mean AGB, in the Congo Basin.** Grey lines are the 10% lowest quantile and black curves are the 90% highest quantile of the variable displayed in the title (representing the modifier variable) interacting with the x-axis variable. We show the effects of

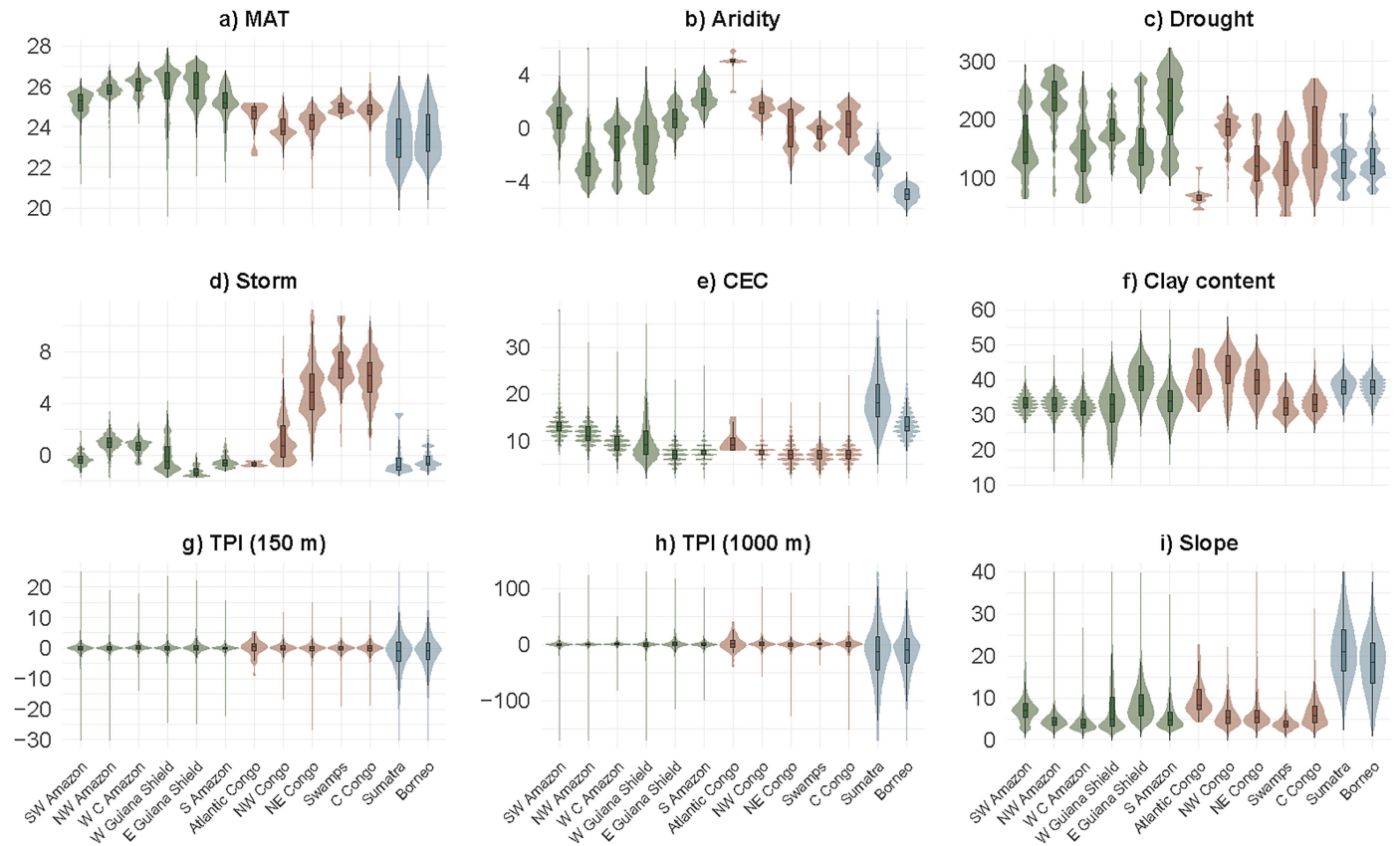
a) ln(MAT) with ln(CEC); b) ln(MAT) with aridity; c) ln(MAT) with TPI at 150 m scale; d) ln(MAT) with soil clay content; e) aridity with ln(MAT); f) aridity with soil CEC; g) aridity with slope; h) aridity with TPI at 150 m scale; i) aridity with storms; j) aridity with drought; k) drought with aridity; and l) drought with TPI at 150 m scale. Sample size = 40,306. Predictions were based on LME models.

## Southeast Asia



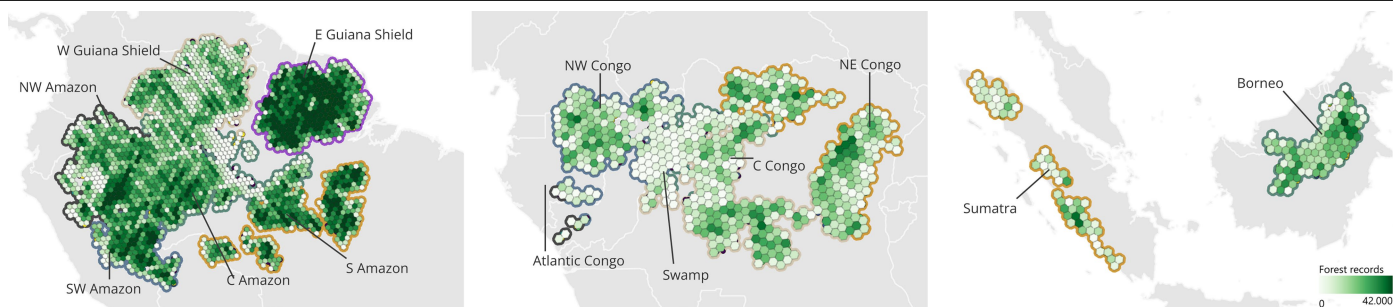
**Extended Data Fig. 8 | Effects of interactions between environmental variables on predicted AGB, relative to the regional mean AGB, in Southeast Asia.** Grey lines are the 10% lowest quantile and black curves are the 90% highest quantile of the variable displayed in the title (representing the modifier variable) interacting with the x-axis variable. We show the effects of a)  $\ln(\text{MAT})$  with

TPI at 150 m scale; b)  $\ln(\text{MAT})$  with aridity; c) aridity with  $\ln(\text{MAT})$ ; d) aridity with storms; e) aridity with soil CEC; f) aridity with drought; g) aridity with slope; h) aridity with TPI at 1000 m scale; i) drought with aridity; j) drought with clay; k) storms with slope; and l) storms with aridity. Sample sizes = 29,436. Predictions were based on LME models.



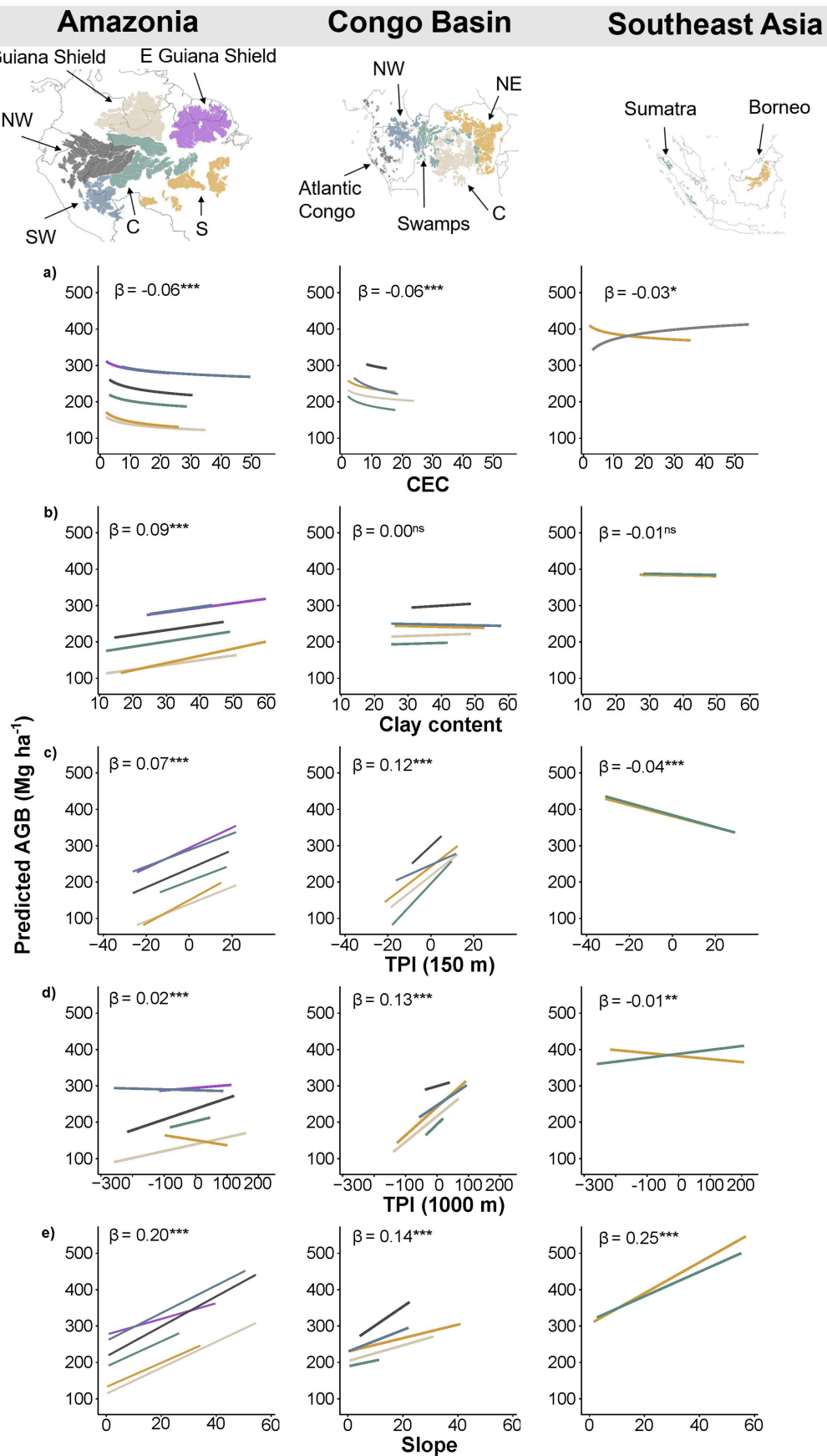
**Extended Data Fig. 9 | Climatic, soil and topographical variability across tropical forests.** Box plot variation of environmental variables across six ecoregions in the Amazon (Northwestern Amazon, Southwestern Amazon, Western Guiana Shield, Central Amazon, eastern Guiana Shield and Southern Amazon), five ecoregions in the Congo Basin (Atlantic coastal forests, Northwestern Congolian, Swamp forests, Central Congolian and Northeastern Congolian) and two ecoregions in Southeast Asia (Sumatra and Borneo). The environmental variables depicted are the ones used explicitly in the LME models: **a)** MAT (°C), **b)** aridity [-], which is the PCA axis of climatic variables

that reflect seasonality, precipitation, solar radiation and water deficit throughout the year, **c)** drought magnitude [-], expressed as absolute values of the cumulative SPEI, **d)** storms [-], based on another PCA axis of CAPE and lightning frequency, **e)** CEC (cmolc kg<sup>-1</sup>), **f)** soil clay content (%), TPI at **g)** 150 m and **h)** 1,000 m resolution [-] and **i)** slope (°). Sample sizes: Amazon  $n \approx 216,667$ ; Congo Basin  $n \approx 40,306$ ; Southeast Asia  $n \approx 29,436$ . In box plots, the centre line indicates the median, box bounds the 25th and 75th percentiles (interquartile range, IQR), and whiskers extend to the most extreme values within  $1.5 \times \text{IQR}$  of the box bounds.



**Extended Data Fig. 10 | Large spatial variation in the number of GEDI footprints across the tropics.** The number of footprints per hexagon reflects the availability of GEDI data (orbital geometry and cloud filtering) and natural

heterogeneity (i.e. rivers, floodplains, natural wetlands) across lowland (between 55 and 900 m elevation) intact landscapes. Each hexagonal point corresponds to a grid cell of  $\sim 1,770 \text{ km}^2$  (approximately  $50 \times 50 \text{ km}$ ).

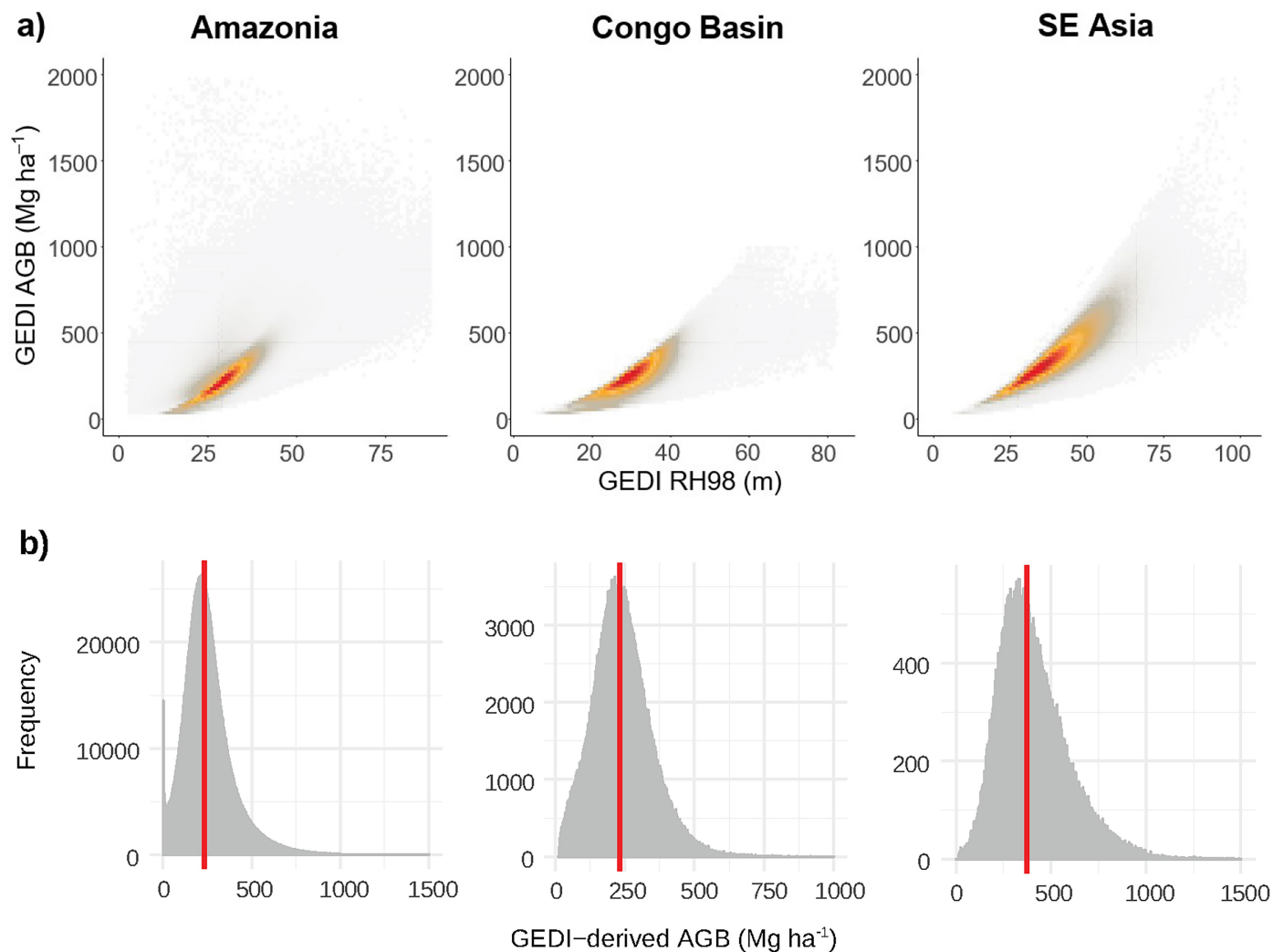


Extended Data Fig. 11 | See next page for caption.

**Extended Data Fig. 11 | Variation in predicted AGB in the Amazon, Congo Basin and Southeast Asia with soil and topography.** Curves are based on AGB predictions from LME modelling with environmental variables and their interactions as fixed effects, obtained by fitting the model to six ecoregions in the Amazon (western Guiana Shield, eastern Guiana Shield, northwestern, southwestern, central and southern Amazonian forests), five ecoregions the Congo Basin (Atlantic coastal forests, swamp forests, northwestern, northeastern and central Congolian forests) and two ecoregions in Southeast Asia (Sumatra and Borneo). The model included spatial random effects, implemented as random effects of 10 × 10 km grid cells nested within ecoregion, to account for spatial autocorrelation in AGB influences due to differences in

species and functional composition and other terms not included in the model. Predicted AGB showed statistical variation with **a)** CEC, **b)** soil clay content, **c)** TPI at 150 m scale, **d)** TPI at 1,000 m scale, and **e)** slope.  $\beta$  is the standardized regression coefficient for their respective environmental variables and their two-sided significance level: ns = non-significant, \*  $p$ -value < 0.05, \*\*  $p$ -value < 0.005,  $p$ -value < 0.005. Exact  $p$ -values are provided in Supplementary Tables 1–3. Sample sizes: Amazon  $n \approx 216,667$ ; Congo Basin  $n \approx 40,306$ ; Southeast Asia  $n \approx 29,436$ . A description and discussion of these soil and topographical relationships with AGB are provided in detail in Supplementary Methods 7.





**Extended Data Fig. 12 | Distribution of AGB estimated from GEDI.**

**a)** Relationships between estimated AGB and 98% relative height across three biogeographical regions in the tropics from the GEDI data for 2020. Colours in the 2D binned density plots represent point density, following a continuous gradient from grey (low density) to red (high density). **b)** Histograms of

estimated AGB from GEDI across the Amazon, Congo Basin and Southeast Asian forests using GEDI data at the footprint level. The vertical solid red lines correspond to the median AGB values. Sample sizes: Amazon  $n \approx 13,747,868$ ; Congo Basin  $n \approx 1,637,208$ ; Southeast Asia  $n \approx 397,734$  footprints.

**Extended Data Table 1 | Environmental variables used to model AGB**

| <b>Variable</b>                                                            | <b>Unit</b>                                  | <b>Source</b> | <b>Spatial resolution</b> | <b>Temporal extant</b> |
|----------------------------------------------------------------------------|----------------------------------------------|---------------|---------------------------|------------------------|
| Mean annual temperature ( <i>MAT</i> )                                     | °C                                           | WorldClim     | 30 arc seconds (~0.0083°) | Jan 1980 - Dec 2019    |
| Mean annual precipitation ( <i>MAP</i> )                                   | mm                                           | CHIRPS        | 0.05°                     | Jan 1981 - Dec 2019    |
| Temperature seasonality ( <i>temp season</i> )                             | °C                                           | WorldClim     | 30 arc seconds (~0.0083°) | Jan 1980 - Dec 2019    |
| Precipitation seasonality ( <i>prec season</i> )                           | mm                                           | CHIRPS        | 0.05°                     | Jan 1981 - Dec 2019    |
| Standardized Precipitation–Evapotranspiration Index ( <i>SPEI</i> )        | [-]                                          | SPEIbase      | 0.05°                     | Jan 1980 - Dec 2019    |
| Maximum Cumulative Water Deficit ( <i>MCWD</i> )                           | mm                                           | CHIRPS        | 0.05°                     | Jan 1981 - Dec 2019    |
| Number of clear days ( <i>clear days</i> )                                 | days                                         | MODIS         | 1000 m (~0.00899°)        | Mar 2000 - Dec 2019    |
| Nº of days with rainfall $\geq 20$ mm ( <i>day20 / heavy rains</i> )       | days                                         | CHIRPS        | 0.05°                     | Jan 2000 - Dec 2019    |
| Nº of months with rainfall $\leq 100$ mm ( <i>month 100 / dry months</i> ) | months                                       | CHIRPS        | 0.05°                     | Jan 2000 - Dec 2019    |
| Convective Available Potential Energy ( <i>CAPE</i> )                      | J kg <sup>-1</sup>                           | ECMWF ERA5    | 31 km (~0.3°)             | Jan 1980 - Dec 2019    |
| Lightning                                                                  | strokes Km <sup>-2</sup> month <sup>-1</sup> | WWLLN         | 0.5°                      | Jan 2010 - Dec 2019    |
| Soil cation exchange capacity ( <i>CEC</i> )                               | cmol <sub>c</sub> Kg <sup>-1</sup>           | ISRIC         | 250 m (~0.00225°)         | -                      |
| Soil clay content ( <i>clay</i> )                                          | %                                            | OpenLandMap   | 250 m (~0.00225°)         | -                      |
| Topographic position index ( <i>TPI</i> )                                  | [-]                                          | SRTM          | 30 m (~0.000269°)         | -                      |
| Slope                                                                      | degrees (°)                                  | SRTM          | 30 m (~0.000269°)         | -                      |

A summary of the environmental variables (and their corresponding abbreviations in italic) included in the model to predict AGB, alongside the data unit, data source, spatial resolution and temporal extant. Because we used GEDI AGB values from January 2020 to December 2020, average values of the climatic variables were calculated at the grid-cell (2.5×2.5-km) level as the mean over a temporal extent. This time interval reflected data availability across intact forest landscapes and ended in December 2019 to ensure that the analysis captured the effects of previous climatic conditions on AGB.

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Our web collection on [statistics for biologists](#) contains articles on many of the points above.

### Software and code

Policy information about [availability of computer code](#)

Data collection Global SPEI database (SPEIbase) version 2.10, available in Google Earth Engine.

Data analysis The LME models were fitted using the lme and varFixed functions in the nlme R package. Variable selection (LASSO) in glmnet R package. Principal Component Analysis in stats R package. Variation Inflation Factors (VIF) from car R package. Random Forest from ranger R package. All these R packages which contain all the above-mentioned R functions used R version number 4.3.2. Codes for running the models can be found at: <https://doi.org/10.5281/zenodo.19474558>

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Source datasets used in this study are publicly available and include NASA GEDI Level 4A aboveground biomass density data (<https://doi.org/10.3334/>

ORNLDAAC/2056), WorldClim climate data (<https://worldclim.org/data/worldclim21.html>), the Global SPEI database (SPEIbase version 2.10; SPEIbase: Standardised Precipitation-Evapotranspiration Index database, Version 2.11 | Earth Engine Data Catalog | Google for Developers), CHIRPS precipitation data (<https://www.chc.ucsb.edu/data/chirps>), the CHIRPS-derived Maximum Cumulative Water Deficit dataset (<https://doi.org/10.5281/zenodo.4903340>), MODIS MOD09GA Version 6 surface reflectance data (<https://lpdaac.usgs.gov/products/mod09gav061/>), ERA5 reanalysis data (<https://cds.climate.copernicus.eu/datasets/reanalysis-era5-single-levels>), World Wide Lightning Location Network lightning data (<https://doi.org/10.5281/zenodo.10725446>), SoilGrids soil data (<https://soilgrids.org>), OpenLandMap soil data (<https://openlandmap.org>), Shuttle Radar Topography Mission (SRTM) elevation data from NASA Earthdata (<https://earthdata.nasa.gov>), and Global Land Analysis and Discovery (GLAD) Intact Forest Landscapes and Global Land Cover datasets (<https://glad.umd.edu>). All processed data required to reproduce the analyses are available in the Zenodo repository.

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## Ecological, evolutionary & environmental sciences study design

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|                          |                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
|--------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Study description        | We used 286,409 estimates of aggregated aboveground biomass (AGB) from GEDI (a NASA LiDAR space mission) across 3 tropical biogeographical regions (Amazonia, Congo Basin and Southeast Asia) to predict climate, soil and topographic effects on AGB. Predictions were made using linear mixed-effects models (LME), with a 50 x 50 km grid nested within ecoregion as random factors. We tested interactions among all variables in the LME models. |
| Research sample          | Our sample was all intact lowland forests across all tropical regions. We removed montane and coastal forests, as well as wetlands. We obtained GEDI data from year 2020 across all the areas as we had a map of disturbance for that year. By doing so, we minimized any additional disturbances that happened to any intact forests across the tropical region after 2020.                                                                          |
| Sampling strategy        | We used GEDI data that is on orbit in the International Space Station. GEDI covers all areas across the tropics, consistently mapping areas that are of difficult access to reach. We used all data collected for year 2020, which resulted in 16 million measurements of forest structure and estimates of aboveground biomass. Data were then aggregated. We used the aggregated data to develop our models.                                        |
| Data collection          | Data were made directly available to the GEDI team, of which the corresponding authors and PI are members and co-authors of this paper.                                                                                                                                                                                                                                                                                                               |
| Timing and spatial scale | We obtained GEDI data from year 2020 (January 1 2020 - December 31 2020) across all the areas as we had a map of disturbance for that year. By doing so, we minimized any additional disturbances that happened to any intact forests across the tropical region after 2020.                                                                                                                                                                          |
| Data exclusions          | Any data that had canopy heights above 88 m in the Amazon, 82 m in the Congo Basin and 101 m in Southeast Asia were excluded, as these height thresholds exceed the maximum canopy heights observed for each region.                                                                                                                                                                                                                                  |
| Reproducibility          | Attempts to repeat the experiment were successful                                                                                                                                                                                                                                                                                                                                                                                                     |
| Randomization            | We separated each biogeographical region (Amazon, Congo Basin and Southeast Asia) into subgroups called ecoregions. Each ecoregion has distinct environmental characteristics that modulate species and functional composition. Therefore, we separated these biogeographical regions into ecoregions based on species and functional similarities based on previous works.                                                                           |

Blinding

One of the key advantages of using a spaceborne LiDAR is that we can have a greater spatial coverage. We included a grid of 50 x 50 km as random factor to account for potential autocorrelation, which could otherwise lead to biased estimates of the fixed effects.

Did the study involve field work? ☐ Yes ☒ No

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